DISENTANGLING THE EFFECTS OF MULTIPLE ECOSYSTEM CHANGES ON FISH POPULATION AND COMMUNITY DYNAMICS

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DISENTANGLING THE EFFECTS OF MULTIPLE ECOSYSTEM CHANGES ON FISH POPULATION AND COMMUNITY DYNAMICS

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North temperate lakes are undergoing diverse physical, chemical, and biological changes, including warming water temperatures, shifts in lake trophic states, and introductions of non-native species. These ecosystem perturbations rarely occur in isolation, making it difficult to evaluate the impacts of concurrent perturbations on population and community dynamics. Here, I use Oneida Lake, New York, USA, to study interactions among multiple ecological changes and their combined effects on age-0 and juvenile yellow perch (*Perca flavescens*). These ecological changes included diversification of the predator and prey communities, shifts in lake trophic state from eutrophic to mesotrophic, and an expansion of littoral habitats. Multiple long-term limnological and fisheries datasets were integrated with short-term diet studies of age-0 yellow perch and their predators from nearshore and offshore habitats to develop a multi-habitat understanding of lake-wide responses to ecosystem perturbations.

Walleye (*Sander vitreus*) were still the most important predator on age-0 and juvenile yellow perch, though the importance of alternative predators, such as white perch (*Morone americana*), smallmouth bass (*Micropterus dolomieu*), and largemouth bass (*Micropterus salmoides*), was also high and has likely increased. Consumption

of age-0 yellow perch was dominated by walleye and white perch in offshore habitats during early summer, but transitioned to walleye, smallmouth bass, and largemouth bass in nearshore habitats during the fall and second year of life. As ecological conditions within the lake changed, age-0 yellow perch population dynamics became increasingly driven by littoral habitats and the population-level reliance on benthic energy pathways increased from 10-20% in the 1960s to 30-70% in the 2000s. These results illustrate the importance of both nearshore and offshore habitats to age-0 and juvenile yellow perch population dynamics and highlight the complexity of population- and community-level responses to ecosystem perturbations.

BIOGRAPHICAL SKETCH

William was born on August 30, 1982 in Brookfield, Wisconsin to Frank and Sandie Fetzer. He grew up in Nashotah, Wisconsin, where he learned to love the outdoors and appreciate the value of nature through his experiences hunting and fishing with his family, especially his father, brother and god-father.

William graduated from Arrowhead Union High School in 2001 and enrolled at the University of Wisconsin-Madison to pursue a degree in Wildlife Ecology. While at Wisconsin, he received an NSF-REU to work with Dr. M. Jake Vander Zanden at the Center for Limnology for the summer of 2003. After the summer, he switched majors to Zoology, focused his coursework on aquatic ecology, and continued working for Dr. Vander Zanden. In 2005, William graduated with honors from the University of Wisconsin-Madison with a degree in Zoology and enrolled in a MS/PhD program at Cornell University in Natural Resources. He completed a Master's of Science studying over-winter mortality of age-0 fish in 2009, under the guidance of Dr. Lars G. Rudstam and Dr. James R. Jackson. William stayed in the Department of Natural Resources at Cornell University to pursue his doctorate, and continued working on food web dynamics in Oneida Lake, NY. On August 18, 2012, he married Sarah Michelle Collins on the Point at the Cornell Biological Field Station.

To my godfather, Keith Lee Marshall.

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This work would not have been possible without considerable effort from many individuals. Tom Brooking, John Forney, JoAnne Getchonis, Kristen Holeck, Scott Kruger, Jonathan Swan, Tony VanDeValk and Brian Young made significant contributions throughout all aspects of this research, and repeatedly helped me maintain my motivation and sense of humor. Many wonderful interns provided valuable assistance with field sampling and sample processing, including Alex Caillat, Paul Clerkin, Collin Farrell, Mark Leopold, Maggie Luebs, Derek West, and Katie White. Numerous graduate students enhanced my experiences at the CBFS and Cornell and engaged in frequent fishy conversations, particularly Dan Bogan, Ed Camp, Sam Chamberlain, Chris Dalton, Ben Dalziel, Robin DeBruyne, Chaz Hyseni, Ezra Lencer, Jesse Lepak, Jason Robinson, T.J. Ross, Paul Simonin, Joe Simonis, Claire Ingel, and Elise Zipkin. Sarah Collins assisted me throughout all aspects of this project, but most importantly, provided encouragement when I needed it most. I am indebted to her.

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PREFACE

Anthropogenic impacts to ecosystem structure and function are widespread; including land transformation, biotic additions and losses, modified biogeochemical cycles, loss of biodiversity, and climate change (Vitousek *et al.* 1997). Ecosystem perturbations rarely occur in isolation, making it difficult to: 1) understand the direct and indirect effects of individual stressors on ecosystem structure and function, 2) identify complex interactions between multiple stressors, and 3) develop management and policy strategies for addressing these stressors across broad temporal and spatial scales. Ensuring continued provisioning of ecosystem services, such as fisheries, to the growing human population requires that these challenges are addressed in creative ways that acknowledge the complexities driving feedbacks within ecological systems.

Lakes represent ideal ecosystems to study interactions between multiple ecosystem stressors because their boundaries are relatively well-defined. Current changes occurring in lake ecosystems include changes in productivity, introductions of non-native species, climate change, shifts in species composition, and fluctuating water levels. Increased water clarity is primarily driven by widespread nutrient loading reductions and the introduction of dreissenid mussels (zebra mussels (*Dreissena polymorpha*) and quagga mussels (*Dreissena rostriformis bugensis*); Vanderploeg *et al.* 2002; Dobiesz and Lester 2009). Greater light penetration stimulates macrophyte and benthic algae growth, elevating the importance of benthic energy pathways in supporting secondary production within lake ecosystems (Mills *et al.* 2003; Zhu *et al.* 2006; Higgins and Vander Zanden 2010). Additionally, dreissenid mussels can directly influence primary and secondary benthic production through pseudofeces deposition, coupling benthic and pelagic food webs (MacIsaac 1996; Karatayev *et al.* 1997; Ricciardi *et al.* 1997). As a result of these changes, many lakes have or are undergoing oligotrophication or benthification, characterized by decreases

in ecosystem productivity and/or shifts from pelagic to benthic production (Mills *et al.* 2003, Zhu *et al.* 2006). Despite the many observed effects of water clarity increases on lower trophic levels and habitat distributions, impacts to higher trophic levels, specifically fish, are difficult to assess and often inconsistent (Higgins and Vander Zanden 2010).

Fish responses to changing ecological conditions are complex because fish are mobile, utilize multiple habitats, and integrate both benthic and pelagic production (Vander Zanden and Vadeboncoeur 2002). Several studies show changes in growth and abundance of fish populations following increased water clarity (Karatayev and Burlakova 1995; Maceina and Bayne 2001; Hoyle *et al.* 2008; Irwin *et al.* 2009), while others do not (Dermott *et al.* 1999; Trometer and Busch 1999; Mayer *et al.* 2000). Higher water clarity is often correlated with shifts in fish species composition from pelagic to littoral and benthic species over temporal (Strayer *et al.* 2004, Robillard and Fox 2006; Irwin *et al. in press*) and landscape scales (Nate *et al.* 2003; Lester *et al.* 2004). Despite widespread spatial and temporal patterns demonstrating the relationship between water clarity and fish communities, mechanisms driving patterns or the subsequent effects to population and community dynamics are currently unknown or speculative.

Few previous studies have taken a multiple habitat approach to understanding how multiple ecosystem perturbations interact to drive fish population- and community-level responses. Many fish occupy multiple habitats. Demographic rates, such as growth and mortality, are often different across habitat types, making habitat heterogeneity and selection key drivers of population and community dynamics (Brandt *et al.* 1992; Jeppesen *et al.* 1998; Hayes *et al.* 2009). Responses of fish populations and communities to ecosystem perturbations are the combined inter- and intra-specific interactions occurring across limnetic, demersal, and littoral habitats.

Differential ability to adapt habitat selection strategies to changes in habitat and resource availability could explain inconsistencies observed across species and systems. Fish populations able to adjust habitat selection to changing conditions may demonstrate resilience, while habitat specialist are likely to either increase or decrease depending on the specific habitat they occupy (i.e. littoral increase; pelagic decrease if water clarity increases). Here, I employ a multiple habitat approach to understand the complexity of fish population responses to ecosystem perturbations and evaluate alternative explanations of the mechanisms driving observed trends. I focus on how changes in predator and prey communities, water clarity increases, and expansions of littoral habitats affect age-0 yellow perch population dynamics across life stages in limnetic, demersal, and littoral habitats of Oneida Lake, New York.

STUDY SITE

The Cornell Biological Field Station (CBFS) on Oneida Lake, NY (area ~207 km^2, maximum depth ~16.6 m, mean depth ~6.8 m) provides a rare opportunity to investigate interactions between multiple ecosystem changes and fish population and community dynamics. CBFS researchers have collected limnological and fisheries data on the lake for over 50 years, building a comprehensive dataset and library of archived samples across multiple habitats and life history stages. Fish community sampling is designed to track abundances of percids (walleye (*Sander vitreus*) and yellow perch (*Perca flavescens*)), which have historically been the primary predator and prey in the lake, respectively (Forney 1976; Forney 1977).

Percids are sampled across life stages, from larvae through adulthood; including 18 mm (larval stage), August 1 (beginning of demersal stage), October 15 (end of first growing season), May 1 (abundance at age-1), and throughout adulthood (see Irwin *et al.* in press for complete description). This dataset has been instrumental

in advancing aquatic and fisheries science (Forney 1976; Mills and Forney 1983; Mills and Forney 1988, Rose *et al.* 1999) and demonstrating the effects of ecological perturbations on aquatic ecosystem structure and function: including nutrient reductions and introduction of non-native species (*e.g.,* zebra mussels; Mayer *et al.* 2000; Zhu *et al.* 2006; Irwin *et al.* 2009, Irwin *et al. in press*), changes in forage fish (Fitzgerald *et al.* 2006), climate effects on fish populations (Fitzgerald *et al.* 2006; Jackson *et al.* 2008), and fish consumption by Double-crested Cormorants (*Phalacrocorax auritus*; Rudstam *et al*. 2004).

Recently, Irwin *et al.* (2009; *in press*) summarized patterns in the long-term fisheries dataset, looking at population dynamics of age-0 yellow perch in offshore habitats (limnetic and demersal) and changes in community composition following the ecosystem perturbations described in the previous paragraph. Across the dataset, age-0 yellow perch abundance was lower across all life stages. Mortality increased from the larval stage to the demersal stage (18 mm – Aug. 1) and decreased throughout the demersal stage (Aug. 1 – Oct. 15). Overall, the age-0 yellow perch growth rate increased and was density-dependent. Despite reduced age-0 abundance, age-1 abundance remained stable (Fitzgerald *et al.* 2006).

Identifying the driver of these changes is challenging because several perturbations to the lake occurred during a similar time period: including more frequent recruitment of alternative forage (*e.g.,* gizzard shad (*Dorosoma cepedianum)* and white perch (*Morone americana*); Fitzgerald *et al.* 2006), increased predator diversity (white perch, smallmouth bass (*Micropterus dolomieu*), and largemouth bass (*Micropterus salmoides*); Irwin *et al. in press*), and increased water clarity with subsequent increases in complexity and distribution of littoral habitats (Zhu *et al.* 2006).

SUMMARY OF MAIN FINDINGS

Importance of multiple habitats

This research represents a step-forward towards further incorporation of habitat-specific processes into the functioning of lake ecosystems and modeling of fish populations in Oneida Lake (Rose *et al.* 1999, Rutherford *et al.* 1999, Sable and Rose 2008, Jaeger Miehls *et al.* 2009) and other lakes (Hayes *et al.* 2009). Previous analyses of the effects of dreissenid introductions on fish populations and communities have been inconsistent (Higgins and Vander Zanden 2010) and have predominantly only looked at one habitat type (Strayer *et. al.* 2004, Robillard and Fox 2006; Irwin *et al. in press*). These previous studies do not address that fish use multiple habitats (Vander Zanden and Vadeboncoeur 2002) and population responses to ecosystem perturbations may be habitat-specific. Throughout this dissertation, integrating information from multiple habitats allowed me to draw more robust conclusions about population and community dynamics than would have been possible with information from only one habitat.

In Chapter 1, I was able to demonstrate seasonal differences in consumption dynamics of walleye, smallmouth bass, and largemouth bass across nearshore and offshore habitats. Previous analyses were based on the assumption that the population dynamics of yellow perch are primarily driven by offshore habitats (Forney 1977; Nielsen 1980; Lantry *et al.* 2008). This dissertation demonstrates that offshore predation is still very important during early summer, but decreases throughout the fall. During the second half of the growing season and throughout the second year of life, predation on yellow perch is dominated by nearshore habitats. The extent of nearshore predation has likely increased over time, and suggests an additional source of mortality that is likely contributing to the lack of adult yellow perch population

recovery to cormorant hazing in Oneida Lake.

Chapter 2 illustrates the difficulty of drawing conclusions based on information from only one habitat. In this chapter, I aimed to test whether benthivory, planktivory, and piscivory by yellow perch and white perch were affected by water clarity. These analyses were limited to data available through the long-term Oneida Lake gillnet survey, when yellow perch and white perch overlapped in time and space. Though I was able to provide evidence suggesting greater divergence of foraging strategies between these two species during periods of low water clarity, conclusions could be more robust by incorporating data from limnetic habitats. This would help identify changes in catch rates and foraging across habitats to better understand population and lake-wide changes in these two species.

In Chapter 3, I show habitat-specific responses of age-0 yellow perch to ecosystem state shifts can be asymmetrical. Previous analyses of age-0 yellow perch responses to ecosystem changes have been limited to offshore habitats (Mayer *et al.* 2000; Irwin *et al.* 2009). I find that demersal age-0 yellow perch exhibit no change in their use of pelagic energy pathways and their density declined over time. By incorporating information from littoral habitats, an alternative explanation emerged. As water clarity increased, demersal populations declined while littoral populations remained stable or increased. As a result, the relative importance of each habitat to population dynamics shifted, and littoral habitats began to dominate recruitment dynamics of age-0 yellow perch. With this shift, age-0 yellow perch production became less reliant on pelagic energy pathways and more reliant on benthic energy pathways. This demonstrates the plasticity of fish to respond to ecosystem perturbations, and highlights the complexity of population-level responses to large-scale ecosystem perturbations.

Diversification of predator community

Increases in predator diversity can impact prey fish communities beyond increasing consumptive demand. Differences in predator morphology, behavior, and spatial distributions can limit prey supply to predators and modify the spatial and temporal impacts of predators on their prey. As predatory fish diversity increases, prey fish may be exposed to predators during life history stages that were historically not susceptible to predation and/or the availability of predator refuges may be reduced. In addition to increases in numbers, changing ecological conditions can shift the competitive advantage between predators and prey and cause previously unimportant predators to consume more prey fish.

In Oneida Lake, NY, the predator-prey dynamics have historically been driven by walleye-yellow perch interactions (Forney 1977; Forney 1980). Long-term trends in age-0 yellow perch demonstrate offshore mortality has increased during early summer but declined later in the growing season (Irwin *et al.* 2009). Interestingly, results of Chapter 1 demonstrate that the amount of mortality that can be attributed to walleye has decreased substantially since the 1970s (Forney 1977). This dissertation provides strong evidence that white perch, largemouth bass and smallmouth bass are now accounting for a greater proportion of yellow perch mortality. As predator diversity has increased, the first few years of life for yellow perch are now a gauntlet of hungry mouths that limit the availability of spatial and temporal refuges from predation.

During the limnetic stage, walleye consume the greatest numbers of age-0 yellow perch, but this is also the time when the most mortality was not accounted for in Chapter 1. Interestingly, this time period corresponds with the timing of white perch predation on age-0 yellow perch in Chapter 2 and suggests that white perch foraging efficiency on age-0 yellow perch may be positively correlated with water

clarity. As a result of the intense predation on age-0 yellow perch during the limnetic period, their distributions are primarily limited to littoral habitats through mid-summer and into the fall (Chapter 3). In these habitats, walleye, smallmouth bass, and largemouth bass consume age-0 yellow perch, reducing the suitability of these habitats as refuges from predation. Predation in littoral habitats continues throughout the second year of life. Across all predators, the extent of predation increases at higher age-0 yellow perch densities, which may limit the production of large year-classes and stabilize recruitment dynamics if mortality rates are high enough.

Resilience of populations to ecosystem perturbations

Chapter 3 sheds new light on interactions between individual specialization, ecosystem states, and population density, and the effect these interactions have on population dynamics. Most previous studies aim to identify environmental conditions that lead to individual specialization, focusing on the role of population density (Svanbäck and Persson 2009; Pfenning *et al.* 2007). Despite a growing understanding of how individual specialization develops, little is known about the subsequent effects to population dynamics (Rueffler *et al.* 2006).

Results from Chapter 3 suggest fish that employ multiple life history strategies can diversify the ecological conditions for which a subset of a population is adapted. These populations are thereby more resilient to ecosystem perturbations through changes in the relative importance of strategies better adapted to changing habitat and resource distributions. In Oneida Lake, the distribution of individual specialists in the age-0 yellow perch population shifted from pelagic specialists to benthic specialists as the lake transitioned from a eutrophic to mesotrophic state. This shift demonstrates the ability of age-0 yellow perch to adapt to changing ecological conditions, and likely contributes to the stability of age-1 yellow perch population dynamics (Fitzgerald *et*

al. 2006).

RECOMMENDATIONS

The questions asked in this dissertation were possible because of the wealth of long-term data available for Oneida Lake. This dataset is unique among freshwater lakes of the world, and the current monitoring program should be continued in to the future to maintain Oneida Lake as a model system for studying how individuals, populations, communities, and ecosystems respond to ecological perturbations. In Chapter 4, I discuss development of a Managers' Model for Oneida Lake in the context of graduate student training. Through this exercise, I am able to place my research within the broader context of the Oneida Lake socio-ecological system, and identify additional research and monitoring that could help develop management objectives and strategies. I suggest three areas where the current monitoring program could be improved:

First, efforts should be made to maximize the amount of information gained from each fish analyzed. This dissertation demonstrates the value of individual fish stable isotope ratios and diet studies to understand changing ecological dynamics. Current advancements in fisheries sciences and analytical tools should be incorporated into the monitoring program to address current and future questions, including the archival of samples from additional surveys and a greater use of stable isotopes and genetic techniques to detect meta-populations, among others.

Second, monitoring programs designed when the lake was eutrophic should be expanded to reflect the greater importance of littoral habitats and benthic energy pathways in driving lake-wide dynamics. This expansion could build on data collected through this dissertation, including continuation of the seine survey and more frequent assessments of nearshore predator communities.

Third, greater efforts should be made to characterize the diversity of stakeholder values, perceptions, and satisfaction with the current state and management of the Oneida Lake socio-ecological system. This could help researchers and managers collectively develop management objectives that incorporate interactions between social and ecological components of the Oneida Lake management system.

Though these recommendations will increase the already limited time and financial resources of the long-term monitoring program, I feel their value is worth the additional investment. I am confident that the staff of the Cornell Biological Field Station and the New York State Department of Environmental Conservation will demonstrate the creativity necessary to move the Oneida Lake monitoring program into the future.

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CHAPTER 1

SPATIAL AND TEMPORAL EFFECTS OF MULTIPLE PREDATORS ON POPULATION DYNAMICS OF A SHARED PREY

ABSTRACT

Recent changes in temperature, light penetration, and distribution of littoral habitats have resulted in transitions from lakes dominated by walleye (*Sander vitreus*) to lakes with multiple predators, including smallmouth bass (*Micropterus dolomieu*) and largemouth bass (*Micropterus salmoides*). These species may compete for shared resources. Here, I focus on competitive interactions between walleye, smallmouth bass, and largemouth bass, and their combined impact on a shared prey, yellow perch (*Perca flavescens*), in Oneida Lake, New York, USA. Growth rates and habitat-specific diet compositions were integrated with temperature and habitat-specific population densities to estimate annual consumption of age-0 and age-1 yellow perch by all three species using the Wisconsin bioenergetics model. Model simulations illustrated that walleye were the dominant predator on age-0 and age-1 yellow perch in both offshore and nearshore habitats; however, smallmouth and largemouth bass also consumed large proportions of both age classes in the nearshore. Consumption across all three species accounted for observed age-0 yellow perch mortality in the late summer and fall, but not in the early summer, suggesting additional sources of mortality on the smallest age-0 yellow perch. Despite similar foraging patterns across predators, analyses of predator growth rates suggest competition for shared prey is

limited. These results are important for understanding how shifts in predator communities can influence population dynamics of a shared prey.

INTRODUCTION

Freshwater lakes across North America are undergoing diverse physical, chemical, and biological changes (Carpenter *et al.* 2011), which have the potential to impact fish communities. Nutrient reductions and the introduction of dreissenid mussels have increased water clarity (Vanderploeg *et al.* 2002; Dobiesz and Lester 2009), which correlates with species composition at broad spatial scales (Nate *et al.* 2003; Lester *et al.* 2004). Additionally, warming water temperatures reduce thermal niche and habitat availability for cool water species, such as walleye (*Sander vitreus*; Wuellner *et al.* 2010), while warm water species, such as smallmouth bass (*Micropterus dolomieui*) and largemouth bass (*Micropterus salmoides*; hereafter black bass when referring to both species), may benefit from warmer water temperatures. Several recent publications have documented shifts in sport-fish populations from walleye to black bass correlated with nutrient reductions, dreissenid mussels, and increased water clarity (Robillard and Fox 2006; Hoyle *et al.* 2008; Irwin *et al.* in press). As fish communities in lakes continue to shift, it is important to understand how species interactions are affected and their role in driving community dynamics.

Walleye and smallmouth bass are considered top predators across many temperate lakes in North America, and substantial literature focuses on potential competitive interactions between these two species. Previous studies have indicated that walleye abundances may be inversely related to smallmouth bass abundances

(Johnson and Hale 1977; Inskip and Magnuson 1983), which could be due to predation or competition. Several studies have documented dietary overlap between smallmouth bass and walleye, but did not observe competition between species, such as decreased growth rates, lower condition, or reduced abundances (Fayram *et al.* 2005; Wuellner *et al.* 2010; Wuellner *et al.* 2011). Direct predation by smallmouth bass on walleye is suspected to be a major source of mortality in one Minnesota lake (Johnson and Hale 1977), but widespread documentation of smallmouth predation on walleye or walleye predation on smallmouth bass is limited. Wuellner *et al.* (2011) reported that generalist feeding by smallmouth limits the intensity of competition between these species, and observed inverse abundance relationships are likely driven by environmental factors and not direct interspecific interactions.

Less is understood about the degree of competition between largemouth bass and walleye since fewer studies have evaluated this interaction. This is likely due to less range overlap between largemouth bass and walleye compared to smallmouth bass and walleye. As species composition across north temperate lakes continues to change, this range overlap will likely increase and a better understanding of largemouth bass-walleye interactions will be essential to develop management objectives for these ecologically and economically important species. Both walleye and largemouth bass are considered highly piscivorous, indicating the potential for more intense competition than between walleye and smallmouth bass (Fayram *et al.* 2005). Several studies have documented high predation by largemouth bass on stocked walleye, demonstrating the potential for largemouth bass to be important predators on juvenile walleye (Fayram *et al.* 2005; Santucci and Wahl 1993), but not

always (Freedman *et al.* 2012). Furthermore, largemouth bass have been shown to consume greater numbers of stocked and wild Pacific salmon than smallmouth bass in Lake Washington (Tabor *et al.* 2007). Other studies provide additional support that largemouth bass are more piscivorous than smallmouth bass (Hubert 1997; Hodson *et al.* 1997; Olson and Young 2003; Fayram *et al.* 2005), highlighting the need for more information on potential competitive interactions between walleye and largemouth bass.

Previous research on these three predators is primarily limited to assessment of dietary overlap, and little is known about their combined consumptive effects on temporal and spatial patterns of mortality and population dynamics of a shared prey. This study focuses on the consumption dynamics of walleye, smallmouth bass, and largemouth bass and their combined effect on population dynamics of a shared prey species, yellow perch (*Perca flavescens)* in Oneida Lake, New York. I parameterized bioenergetic simulations with species-specific growth rates, diet composition, temperature, and abundance to estimate population-level consumption of age-0 and age-1 yellow perch by walleye, smallmouth bass, and largemouth bass. Consumption estimates were compared to independent abundance estimates of age-0 and age-1 yellow perch available for Oneida Lake, which allowed me to explore the individual and combined importance of all three predators in driving yellow perch population dynamics.

METHODS

Study site

Oneida Lake, New York, USA, is a large, shallow mesotrophic lake (area: 207 km^2; mean depth: 6.8 m; maximum depth of 16.8 m) that contains a diverse fish community (> 80 species) that is dominated by warm water fishes. The Cornell Biological Field Station (CBFS) has maintained a long-term fisheries and limnological monitoring program on the lake since 1956, providing data across trophic levels and life history stages of multiple fish species. Oneida Lake has gone through a number of changes in recent years, including increasing summer water temperatures (Jackson *et al.* 2008) and the introduction of dreissenid mussels (zebra mussels (*Dreissena polymorpha*) in the early 1990s and quagga mussels (*Dreissena rostriformis bugensis*) in the early 2000s). Increasing water clarity associated with mussels shifted productivity from pelagic to benthic habitats, increased the abundance of aquatic macrophytes, and subsequently increased the extent of the littoral zone (Zhu *et al.* 2006). This expansion increased the amount of suitable habitat for black bass in Oneida Lake, and combined with increasing water temperatures, may explain increases in black bass catches across multiple standardized datasets (Jackson *et al.* 2012; Irwin *et al.* in press).

Field sampling

Published data on Oneida Lake provided information on adult walleye and age-0 yellow perch abundances and growth rates. Adult walleye abundance, age structure, and growth rates were determined through an annual standardized gillnet survey and

semi-annual mark-recapture estimates (Rudstam and Jackson 2012a). Age-0 yellow perch abundance and growth rates were tracked throughout the growing season in pelagic and demersal habitats using a combination of high-speed Miller sampling in June and standardized bottom trawl surveys in July through October (Rudstam *et al.* 2002; Irwin *et al.* 2009; Rudstam and Jackson 2012b). Age-0 yellow perch abundance and growth in littoral habitats were determined using a beach seine (23 m by 1.5 m; 6 mm mesh) at 9 standardized sites. Seine surveys were conducted weekly in July and August, switching to monthly in September and October during 2007-2009 (see Chapter 3 for additional details). Water temperature was continuously recorded throughout the year at depths of 2 and 10 m with a HOBO temperature recorder (Onset Computer Corporation, Bourne, Massachusetts, USA).

To obtain seasonal predator diets, walleye, smallmouth bass, and largemouth bass were collected monthly from June through October in 2007-9 using either electrofishing or trawling. Nearshore habitats were sampled during two nights and two mornings each month using an electrofishing boat (Smith-Root electronics, 354 V pulsed DC current, pulse rate of 60 Hz, 8 A of current into water). Evening sampling consisted of 2 runs of approximately 45 minutes to one hour, starting at sunset and continuing until both runs were completed and all fish were processed. Morning sampling consisted of one run starting 1.5 hours before sunrise. Habitats sampled were concentrated around Shackelton Point on the south-central shoreline of Oneida Lake and consisted of approximately equal distributions of rocky and weedy sites to efficiently capture both black bass species (Figure 1.1). Offshore habitats were sampled two mornings each month with a 12.2-m bottom trawl that was fished at

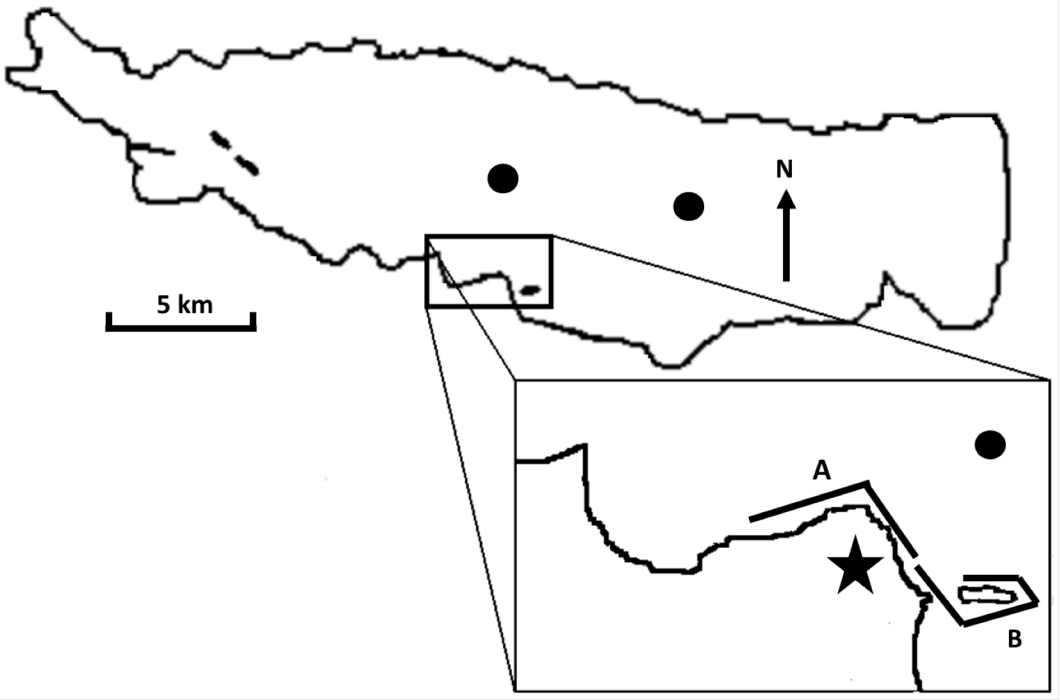

Figure 1.1. Map of Oneida Lake and sampling locations used to collect predator diets. Electrofishing transects (A-B) were located in nearshore habitats within the vicinity of Shackelton Point (indicated with a star). Trawling sites were located in offshore habitats and are indicated with closed circles.

depths between 5-12 m for 15 minutes at three sites (Figure 1.1; see Lantry *et al.* 2008 for more details). During each morning, two sites were sampled immediately following sunrise. In 2006, additional bottom trawl surveys were conducted to aid in the differentiation of the walleye population between nearshore and offshore habitats.

Upon capture, all fish were processed immediately to minimize digestion of stomach contents. Individual fish were anesthetized with MS-222, measured for length, and a scale sample was collected to age fish and back-calculate length-at-age to determine growth rates. Stomach contents were removed via a combination of gastric lavage and acrylic tubes and preserved in 10% formaldehyde. Stomach contents were analyzed in the laboratory, and if possible, all diet items were enumerated, identified to species, and measured for length.

Age and growth analyses

Age and growth for Oneida Lake walleye in Oneida Lake were obtained from previously published data (He *et al.* 2005; He *et al.* in press) *available* through the Knowledge Network for Biocomplexity (Rudstam and Jackson 2012a). To obtain similar estimates for largemouth bass and smallmouth bass, scales were dried and pressed into a cellulose acetate plastic slide to increase the ease of aging and measuring annuli. Slides were magnified using an upright projector and the scale was projected onto a dry erase board. Two readers compared individually determined annuli until a consensus was reached, after which each annuli radius (S_i) and the total scale radius (S_c) were measured from the focus along the antero-lateral axis (Pierce *et al.* 1996). Scales that showed regeneration were not included in the analysis.

Length-at-capture (L_c), S_c, and, S_i were used to back-calculate length-at-age using the Fraser-Lee model with biological intercept (Maceina *et al.* 2007).

$$L_i = \frac{S_i}{S_c}(L_c - c) + c$$

Where L_i is the back-calculated fish body length at age *i,* and *c* represents the length of each species at scale formation (*i.e.,* biological intercept; smallmouth bass: c = 21 mm; largemouth bass: c = 26 mm; obtained from Carlander 1950). Length-at-age was converted to weight using standard length-weight relationships for smallmouth and largemouth bass available for lakes across New York State (smallmouth bass: Ln (weight (g)) = -11.78 + 3.09 · Ln (length (mm)), R^2 = 0.97; largemouth bass: Ln (weight (g)) = -12.51 + 3.23 · Ln (length (mm)), R^2 = 0.98; P.C. Perry *personal communication*). Annual growth in weight was determined as the difference between weight at age-*i* and weight at age-*i* + 1.

Diet composition

Species-specific diet composition was determined as percentage of total diet biomass on a monthly basis. Diet composition for walleye was separated into nearshore and offshore diets based on samples collected through electrofishing and trawling, respectively. Unidentified fish were assigned to species based on the observed composition of identifiable fish. If possible, age-0 and age-1 fish were separated into two categories based on length distributions. Biomass of individual prey items was determined from length-weight relationships available for Oneida Lake (J.L. Forney *unpublished data*), and scaled up to the total proportion of diet based on

the total number of individuals of each species observed in diets for that sampling date. On dates when fish were too digested to obtain length estimates, an estimated length was assigned based on the length estimates from diets collected on proximate sampling dates or length distributions in the lake available through additional datasets (*e.g.,* seine or trawl surveys). For benthic invertebrates, specifically crayfish, length-weight relationships were used to estimate biomass of individual prey items based on the observed length of invertebrates in the diets (Benke *et al.* 1999). Percent composition by biomass for each sampling date within a monthly survey (*e.g.,* two evenings and two mornings electrofishing) was converted into a monthly weighted-average based on the number of diets collected on each specific date. This was to avoid over-representation of dates when few diets were collected.

Population estimation and age-structure

Population estimates for each species were generated using multiple datasets available for Oneida Lake, NY. Previous studies of walleye population dynamics in Oneida Lake provided a good benchmark to estimate smallmouth bass and largemouth bass abundance, which are not as well studied. Age-specific walleye abundance was available through the Knowledge Network for Biocomplexity and was estimated via a long-term gillnet survey complimented with mark-recapture studies every two to three years (Rudstam and Jackson 2012a). To account for seasonal changes in the spatial distribution of the walleye population, a second-order polynomial function was fit to observed changes in catch-per-unit-effort (CPUE) in the 12.2 m bottom trawl survey during 2006-2009. I assumed that seasonal trends in trawl CPUE were a result of

habitat switching and not seasonal changes in trawl catchability. Daily CPUE was scaled to the percent of the walleye population offshore under the assumption that 90% percent of the population was offshore on the first day of simulations. This assumption was generally supported by seasonal CPUE trends in the trawl and electrofishing surveys, which suggested the majority of the walleye population was offshore during early summer. All age classes were assumed to follow the same seasonal trend in nearshore-offshore distribution.

Smallmouth bass were regularly captured in long-term gillnet surveys; however, no mark-recapture studies have been conducted on smallmouth bass since the 1960s (Forney 1972). To overcome this limitation, a gillnet/mark-recapture equation developed for age-4 and older walleye was applied to the gillnet catch of smallmouth bass to estimate the population of age-3 and older smallmouth bass in Oneida Lake, NY (Jackson, J.R. *unpublished data*; Ln(abundance) = 10.163 + 0.592 · Ln (annual gillnet catch)). It was assumed that age-3 and older smallmouth bass and age-4 and older walleye have similar catchabilities and that catchability does not change across ages for smallmouth bass. To determine abundance of age-1 and age-2 smallmouth bass, weighted catch-curve analyses were performed on age-3 and older smallmouth bass pooled across years to provide a general age-structure (Maceina and Bettoli 1998). Weighted catch-curve analyses weigh each observation by the amount of information it contains, reducing the influence of older and rarer age classes. These were used to estimate the proportion of fish in each age class from age-1 to age-8+. The ratio of age-1 and age-2 smallmouth bass relative to age-3 and older fish from the

weighted catch-curve analyses was combined with the age-3+ abundance estimates to determine the total abundance of age-1 and older smallmouth bass in the lake.

Largemouth bass were not consistently caught in any of the long-term monitoring of Oneida Lake, making population estimates difficult. However, angler CPUE of largemouth bass was half of smallmouth bass CPUE (Jackson *et al.* 2012); therefore, it was assumed that largemouth bass were half as abundant as smallmouth bass in Oneida Lake. A weighted catch-curve analysis was also performed for largemouth bass, and used to estimate the proportion of fish in each age class from age-1 to age-8+. Age-specific abundance was determined by multiplying the total population estimate by the proportion of total fish predicted by the catch-curve analysis. These population estimates provided a logical starting point to evaluate population-level consumption of yellow perch by walleye, smallmouth bass, and largemouth bass.

Bioenergetic scenarios

To perform bioenergetics simulations, species-specific growth rates, diet composition, and abundance estimates were used to parameterize bioenergetics models and estimate consumption of age-0 and age-1 yellow perch by nearshore and offshore walleye, smallmouth bass, and largemouth bass. Energy densities of major prey items were obtained from the literature or estimated based on those available for similar species (Lantry *et al.* 2008; Wuellner *et al.* 2010). Model parameters were based on those available in the computer software Fish Bioenergetics 3.0 (Wisconsin bioenergetics model; Hanson *et al.* 1997). Simulations were run for a single

individual from each age class to estimate daily consumption across species over the course of the growing season. Individual daily consumption was then scaled up to the population using population estimates and age structure for each species, assuming no mortality. Population estimates and age structure for walleye differed across years, but were assumed to be the same for black bass.

Diet composition, growth, and water temperatures from high (138,760 ha^{-1}; 2007), medium (125, 621 ha^{-1}; 2009), and low (67,680 ha^{-1}; 2008) age-0 yellow perch densities at 18 mm were used to evaluate interactions between age-0 yellow perch density and the extent of predation. Age-0 yellow perch densities were determined with a high-speed Miller sampler survey (Rudstam and Jackson 2012b) conducted when age-0 yellow perch were approximately 18 mm. Simulations were run with observed diet composition, growth, and water temperatures for those specific years. Growth within a year was based on back-calculated length-at-age from scales collected in the immediate subsequent year (*e.g.,* 2007 growth based on scales collected in 2008). No scales were collected from black bass during 2010 to assess growth rates during 2009. Black bass growth rates for 2009 were based on a Von Bertalanffy growth equation fit separately for each species to all length-at-age data to determine the average age-specific annual growth for both black bass species.

Yellow perch population dynamics

Walleye, smallmouth bass, and largemouth bass consumption estimates from bioenergetics simulations were converted to number of individuals consumed per day by dividing biomass consumed per day by observed age-0 and age-1 yellow perch

individual weights. Daily consumption estimates were compared with age-0 and age-1 yellow perch density estimates to evaluate the relative importance of each predator on yellow perch population dynamics. These analyses were used to determine the proportion of total age-0 and age-1 yellow perch mortality that could be accounted for by each predator, and to assess the potential importance of additional predators in the lake that were not sampled based on differences between observed mortality and mortality due to study predators. Population dynamics of age-0 yellow perch were determined using density estimates available through the high-speed Miller sampler, bottom trawl, and seine surveys. Less data for age-1 yellow perch was available; therefore, consumption estimates were compared to the density of age-1 yellow perch at the start of their second growing season (May 1st).

To account for ontogenetic changes in habitat use by age-0 yellow perch, abundance estimates were broken into two stages. During the limnetic stage, defined as the interval of growth between 18 mm and approximately 45 mm (~1.0 grams), it was assumed that age-0 yellow perch were homogenously distributed across Oneida Lake. Density was estimated once during the limnetic stage when age-0 yellow perch were 18 mm using high-speed Miller samplers (Rudstam and Jackson 2012b). During the littoral/demersal stage, defined as the interval of growth from 45 mm through the fall, it was assumed that age-0 yellow perch were heterogeneously distributed across littoral and demersal habitats (bottom trawl/seine). During this time period, littoral and demersal catch-curves were calculated independently based on the natural log of density estimates available from the seine and trawl surveys. Littoral and demersal catch-curves were then combined using a weighted-average of density (kg/ha) based

on current projections of littoral/demersal spatial coverage in the lake (littoral = 43%; demersal = 57%; Fitzgerald *et al.* in press). During the limnetic period, a constant instantaneous mortality was assumed from the timing of the 18 mm survey to July 15 (start of littoral/demersal stage) and calculated based on observed decreases in abundance. To provide a realistic representation of the transition between the limnetic and littoral/demersal, daily instantaneous mortality throughout the growing season was based on a 20-day moving average across dates. This prevented an abrupt decrease in daily mortality as fish transitioned from the limnetic to the littoral/demersal stage and did not affect mortality at the beginning or end of the growing season.

RESULTS

Diet composition

During 2007-2009, diets were collected from 2,412 walleye, smallmouth bass, and largemouth bass in Oneida Lake, NY (Table 1.1). Walleye were the most common species captured in both nearshore and offshore habitats with 1,052 and 779 total fish caught, respectively. A similar number of largemouth bass and smallmouth bass were collected across years, totaling 294 and 287 fish, respectively. Seasonal diet compositions varied across species and years; but were dominated by age-0 yellow perch, age-1 yellow perch, age-0 gizzard shad (*Dorosoma cepedianum*), crayfish, pumpkinseed sunfish (*Lepomis gibbosus*), and brown bullhead (*Ameiurus nebulosus*; Table 1.1). Across species, increasing diet diversity was associated with weak year-classes of age-0 yellow perch.

Table 1.1. Walleye, smallmouth bass, and largemouth bass monthly diet composition. Percent composition by biomass of walleye (WE), smallmouth bass (SMB), and largemouth bass (LMB) diets used to inform bioenergetics simulations. Major diet items include yellow perch (YP), gizzard shad (GIZZ), crayfish (CRAY), pumpkinseed (PS), and brown bullhead (BBH). Footnotes indicate major species when "other" category exceeds 10% of diet and include emerald shiner[1], age-0 smallmouth bass[2], age-0 tessellated darter[3], trout perch (*Percopsis omiscomaycus*)[4], age-0 white perch[5], and age-0 white sucker[6].

Year	Habitat	Species	Month	n	Age-0 YP	Age-1 YP	Age-0 GIZZ	CRAY	PS	BBH	Other
2007	nearshore	LMB	June	41	1	95					4
			July	36	52	29		14	5	< 1	
			August	8	100						
			September	8	85			15			
			October	20	64		25	10		< 1	
		SMB	June	25	32	24		23			21 [3]
			July	17	21			74			5
			August	14	15			85			
			September	15	52			36			11 [5]
			October	33	32		27	41			< 1
		WE	June	29	64	34					1
			July	52	81	15		2	< 1	0	< 1
			August	92	98				< 1	< 1	2
			September	67	92	5		2	< 1		< 1
			October	126	18	2	77		< 1	3	1
	offshore	WE	June	47	96	4					< 1
			July	63	88	8	3				1
			August	23	29	28	30		< 1		13 [4]
			September	53	70		30				
			October	45	5	1	93				1
2008	nearshore	LMB	June	15	8	61		18	14		< 1
			July	15	5	41		52		1	
			August	6				67		33	
			September	27	23	32	12	10		18	5
			October	34			70	17	2	11	
		SMB	June	30	10	4		85			< 1
			July	13	16			84			< 1
			August	3				1			
			September	17			56	25	7	12	
			October	16			60	12	18		10 [6]
		WE	June	35	59	36					5
			July	58	43	55			< 1	< 1	2
			August	52	18	32	34			6	9
			September	47	24	3	60				13 [2]
			October	98	9	< 1	90		< 1		< 1
	offshore	WE	June	65	99						< 1
			July	44	36		48		< 1		15 [5]
			August	30	10		84				5
			September	29			100				
			October	100	6	2	89				3
2009	nearshore	LMB	June	16		52		12	12	12	
			July	29	20	66		10		4	
			August	4	50			50			
			September	21	33			64			
			October	12	36	18	18	23	5		
		SMB	June	19	14	20		58			5
			July	23	13	6		81			
			August	17	11		27	49			13 [3]
			September	35	4	17	51	28			
			October	10	38	12	28	22			
		WE	June	38	25	24				37	14 [1]
			July	56	24	55			16	5	
			August	30	37	19	35		2		7
			September	68	68	10	4		11		7
			October	204	35	13	52				0
	offshore	WE	June	90	96	1		2			1
			July	54	68	28	0				4
			August	8	6	23	69				2
			September	23	4		89				7
			October	105	5	6	69		1		19 [1,5]

Offshore walleye diets were consistent across years. In early summer, offshore walleye primarily consumed age-0 yellow perch but shifted to age-0 gizzard shad by late fall. Age-1 yellow perch were the only other major diet item observed, as diet diversity was consistently low. Nearshore walleye diets were dominated by age-0 and age-1 yellow perch in early summer, shifting to gizzard shad by late October (Table 1.1). Additional prey items included emerald shiners (*Notropis atherinoides*), age-0 and age-1 pumpkinseed, banded killifish (*Fundulus diaphanus)*, age-0 and age-1 brown bullhead, age-0 walleye, and age-0 smallmouth bass. Diet diversity peaked in June and declined throughout the growing season as age-0 yellow perch and age-0 gizzard shad began to dominate diets. In nearshore and offshore habitats, walleye rarely consumed crayfish (Table 1.1).

Yellow perch, gizzard shad, and crayfish dominated smallmouth bass and largemouth bass diets. Crayfish consistently dominated smallmouth bass diets at all times, but age-0 yellow perch were also an important diet item (Table 1.1). Smallmouth bass also consumed age-1 pumpkinseed, banded killifish, age-0 white perch (*Morone americana*), age-0 tessellated darter (*Etheostoma olmstedi*), age-0 brown bullhead, and age-0 white sucker (*Catostomus commersonii*). These minor diet items rarely accounted for greater than 10% of total diet composition as diet diversity was consistently low throughout the growing season. Largemouth bass diets were dominated by age-1 yellow perch in early summer but shifted to age-0 yellow perch, crayfish, and age-0 gizzard shad through mid-summer and into the fall (Table 1.1). Other diet items included emerald shiners, age-0 and age-1 pumpkinseed, banded killifish, age-0 and age-1 brown bullhead, and benthic invertebrates. These prey

species typically accounted for less than 10% of total diet biomass, but were important occasionally. Diet diversity peaked in June, but largemouth bass consistently fed on a variety of fish species throughout the growing season.

Population estimates and age-structure

Walleye were the most abundant predator during the study, ranging in density from 32.1 to 40.5 fish per hectare (Table 1.2). The proportion of the walleye population in offshore habitats was highest in early summer, declined during late summer, and increased throughout the fall (Figure 1.2; CPUE = $0.0091 \cdot (\text{date})^2 - 1.51 \cdot (\text{date}) + 95.6$, $r^2 = 0.48$). Smallmouth bass ranged in density from 14.4 to 20.8 fish per hectare. Largemouth bass density was estimated at 8.8 fish per hectare (Table 1.2).

Age structure for all species followed a typical catch-at-age curve, illustrating decreasing abundance in each age class as age increased, however, in the final age class the abundance increased as all older fish are grouped into that age class (Table 1.2). Some deviations in this pattern were present as dominant year classes aged over time.

Bioenergetics simulations

Seasonal patterns of consumption were consistent with observed diet compositions and were dominated by age-0 yellow perch, age-1 yellow perch, age-0 gizzard shad, and crayfish (Table 1.3; Figure 1.3). Offshore walleye consumption was dominated by age-0 yellow perch in early summer, but shifted to age-0 gizzard shad

Table 1.2. Walleye, smallmouth bass, and largemouth bass age-specific abundance estimates. Density estimates (#·ha^{-1}) for different age-classes of walleye (WE), smallmouth bass (SMB), and largemouth bass (LMB). All age-8 and older smallmouth bass and largemouth bass are included in the age-8 column; all age-6 and older walleye are included in the age-6 column. Density ranges across years are presented in parenthesis in the Total column.

		Age-specific abundance (#·ha^{-1})								
Species	Year	Age-1	Age-2	Age-3	Age-4	Age-5	Age-6	Age-7	Age-8	Total (#·ha^{-1})
LMB	2006-9	2.4	1.7	1.3	0.9	0.7	0.5	0.4	0.9	8.8
SMB	2006-9	3.5	2.8	2.3	1.9	1.6	1.3	1.1	3.0	17.5 (14.4-20.8)
WE	2007	9.5	6.9	4.5	1.3	1.0	16.4			39.6
	2008	4.9	4.2	1.7	4.8	1.1	15.4			32.1
	2009	9.8	5.8	2.7	3.3	4.2	14.6			40.5

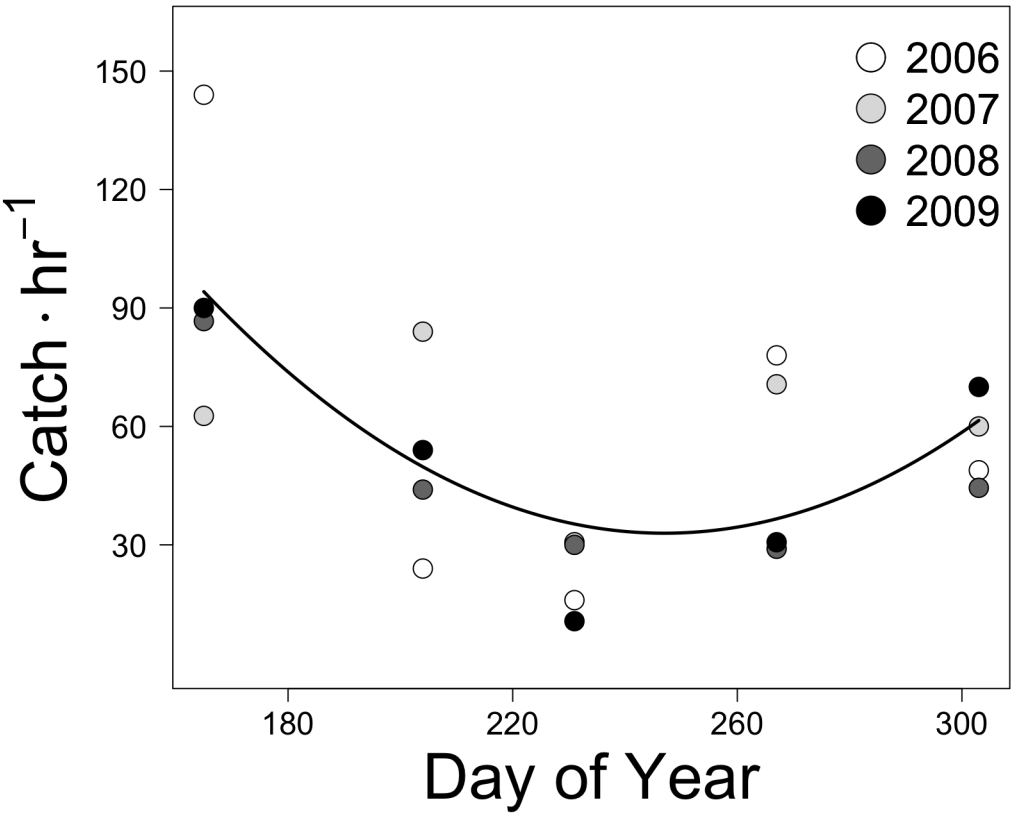

Figure 1.2. Seasonal trends in walleye catch per hour in offshore trawls. Monthly catch rates of walleye in the offshore trawl during 2006-9, with polynomial best-fit line used to assign proportions of walleye population in nearshore and offshore habitats indicated.

Table 1.3. Year- and species-specific consumption estimates of major diet items for walleye, smallmouth bass, and largemouth bass. Walleye (WE), smallmouth bass (SMB), and largemouth bass (LMB) annual consumption ($kg \cdot ha^{-1}$) of age-0 yellow perch (Age-0 YP), age-1 yellow perch (Age-1 YP), crayfish (CRAY), age-0 gizzard shad (Age-0 GIZZ), brown bullhead (BBH), and all other diet items (Other) based on estimates from bioenergetics simulations. Percentage of total annual consumption accounted for by each diet item presented in parenthesis.

Habitat	Species	Year	n	Age-0 YP	Age-1 YP	CRAY	Age-0 GIZZ	BBH	Other	Total
Nearshore	LMB	2007	113	4.37 (67.2)	1.31 (20.1)	0.53 (8.1)	0.15 (2.4)	0.02 (0.4)	0.12 (1.8)	6.50
		2008	97	0.52 (8.2)	1.70 (26.8)	2.45 (38.7)	0.52 (8.2)	0.94 (14.9)	0.20 (3.2)	6.33
		2009	84	1.91 (30.9)	1.54 (24.8)	2.27 (36.6)	0.07 (1.1)	0.16 (2.5)	0.25 (4.1)	6.20
	SMB	2007	104	5.35 (29.0)	0.58 (3.1)	10.94 (59.3)	0.35 (1.9)		1.24 (6.7)	18.47
		2008	79	1.04 (6.0)	0.11 (0.7)	12.60 (72.5)	2.65 (15.3)	0.47 (2.7)	0.49 (2.8)	17.37
		2009	104	1.67 (11.4)	1.22 (8.3)	7.84 (53.4)	3.15 (21.5)		0.80 (5.4)	14.70
	WE	2007	366	13.77 (80.6)	1.26 (7.4)	0.18 (1.1)	1.55 (9.1)	0.10 (0.5)	0.23 (1.3)	17.09
		2008	290	4.16 (27.2)	3.86 (25.2)		5.82 (38.1)	0.31 (2.0)	1.15 (7.5)	15.30
		2009	396	8.05 (42.7)	4.55 (24.1)		3.12 (16.6)	0.72 (3.7)	2.43 (12.9)	18.86
Offshore	WE	2007	231	9.32 (65.5)	1.16 (8.2)		3.45 (24.2)		0.31 (2.1)	14.24
		2008	268	4.29 (34.8)	0.03 (0.2)		7.27 (59.1)		0.72 (5.9)	12.31
		2009	280	6.59 (43.6)	1.95 (12.9)	0.07 (0.5)	5.71 (37.8)		0.79 (5.2)	15.11

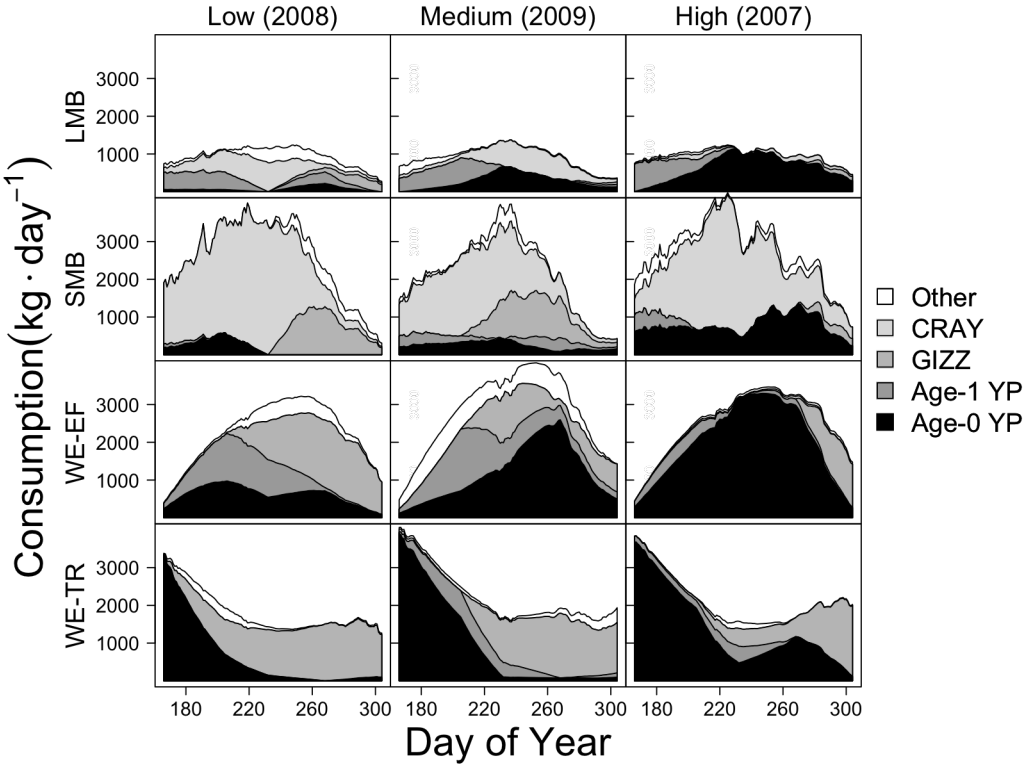

Figure 1.3. Population-level consumption of major diet items by walleye, smallmouth bass, and largemouth bass. Seasonal trends in the consumption of age-0 yellow perch (Age-0 YP), age-1 yellow perch (Age-1 YP), age-0 gizzard shad (GIZZ), crayfish (CRAY), and other (Other) diet items by largemouth bass (LMB), smallmouth bass (SMB), nearshore walleye (WE-EF), and offshore walleye (WE-TR) during years with low (2008), medium (2009), and high (2007) population abundances of age-0 yellow perch.

by fall. Inshore walleye consumption was dominated by age-0 and age-1 yellow perch in early summer, but transitioned to age-0 yellow perch and age-0 gizzard shad in fall. Crayfish dominated smallmouth bass consumption, but age-0 yellow perch and age-0 gizzard shad were important at times. Largemouth bass consumption was dominated by age-0 and age-1 yellow perch, though consumption of crayfish was high in 2008. Across all species, consumption of age-0 yellow perch was highest in 2007 and lowest in 2008, which corresponded to age-0 yellow perch abundance.

Seasonal population-level consumption by walleye across nearshore and offshore habitats was strongly influenced by seasonal patterns in habitat use. In early summer, walleye consumption was dominated by fish in the offshore habitats, but shifted to nearshore habitats as the distribution of the population moved between habitats (Figure 1.3). As a result, consumption of age-0 yellow perch was dominated by offshore habitats in early summer, while nearshore consumption was highest in mid- to late-summer.

Predation on yellow perch

Age-0 yellow perch were an important diet item for walleye, smallmouth bass, and largemouth bass; however, the percentage of total consumption varied across years and was highest in 2007 and lowest in 2008 (Table 1.3; Figure 1.3). For offshore walleye, consumption of age-0 yellow perch by biomass and numbers primarily occurred in early summer (Table 1.3; Figure 1.4). Nearshore walleye and largemouth bass tended to consume the greatest biomass and numbers of age-0 yellow perch during mid- to late summer, while smallmouth bass tended to consume age-0

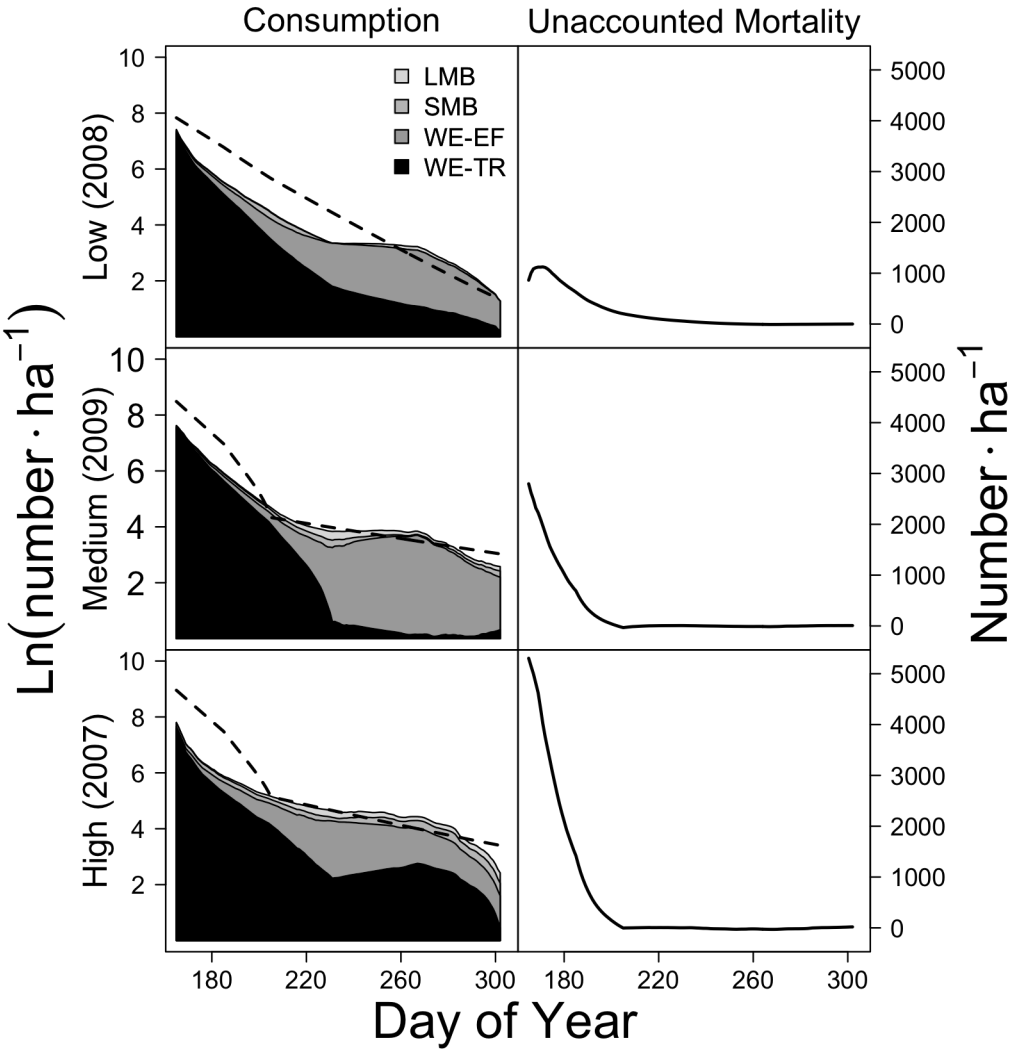

Figure 1.4. Comparison of observed yellow perch mortality and number consumed by walleye, smallmouth bass, and largemouth bass. Seasonal trends in the total number of age-0 yellow perch (as natural log) consumed by offshore walleye (WE-TR), nearshore walleye (WE-EF), smallmouth bass (SMB), and largemouth bass (LMB) during low (2008), medium (2009), and high (2007) population abundances of age-0 yellow perch. Total loss of age-0 yellow perch based on population estimates from 18 mm, trawl, and seine surveys indicated with dashed line. Differences between loss of age-0 yellow perch from population and consumption estimates of walleye, smallmouth bass, and largemouth bass for 2008 , 2009, and 2007.

yellow perch throughout the growing season, except in 2008 (Figure 1.3, 1.4). Consumption of age-1 yellow perch tended to be dominated by nearshore walleye and largemouth bass, but smallmouth bass and offshore walleye were also important predators in most years (Table 1.3; Figure 1.3, 1.5). Consumption of age-1 yellow perch tended to occur during early to mid-summer (Figure 1.5), but the extent of consumption did not show consistent patterns across years (Table 1.3).

Walleye, smallmouth bass, and largemouth bass consumption of age-0 and age-1 yellow perch was an important driver of yellow perch population dynamics (Table 1.4; Figure 1.4). During 2008 and 2009, walleye, smallmouth bass and largemouth bass consumed approximately 40 percent of the total density of age-0 yellow perch available at the start of the bioenergetics simulations, but only 29 percent in 2007. Offshore walleye consumed the highest number of age-0 yellow perch, followed by nearshore walleye, smallmouth bass, and largemouth bass, respectively. This pattern was consistent across all years. Comparisons of observed age-0 yellow perch mortality and consumption estimates showed that the highest unaccounted for mortality was in early summer, but declined to near zero by mid-summer (Figure 1.4). Mortality unaccounted for by the three predators was highest in 2007, when age-0 yellow perch were the most abundant. The number of age-1 yellow perch consumed by walleye, smallmouth bass, and largemouth bass was higher than the density estimate on May 1, suggesting that these predators consume 180-210 percent of the total age-1 population within a given year (Table 1.4). Nearshore walleye had the greatest impact on age-1 yellow perch population dynamics, followed by largemouth bass and offshore walleye. Smallmouth bass had the lowest impact on age-1 yellow

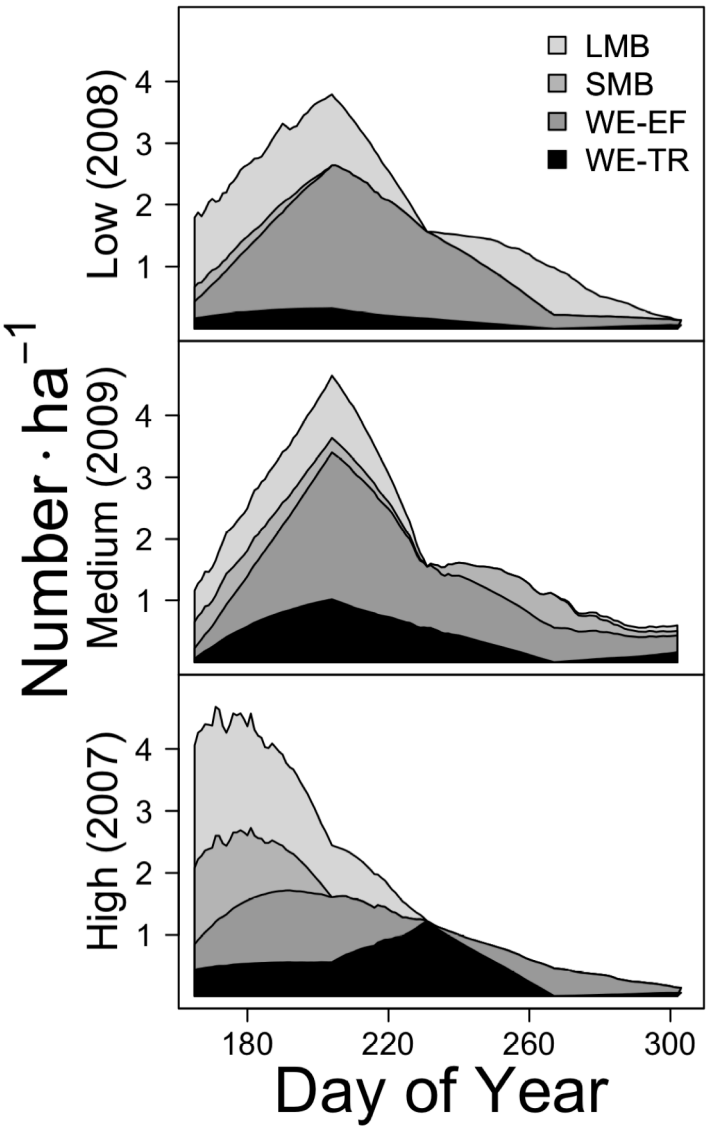

Figure 1.5. Daily consumption of age-1 yellow perch by walleye, smallmouth bass, and largemouth bass. Seasonal trends in the total number of age-1 yellow perch consumed by offshore walleye (WE-TR), nearshore walleye (WE-EF), smallmouth bass (SMB), and largemouth bass (LMB) during low (2008), medium (2009), and high (2007) population abundances of age-0 yellow perch.

Table 1.4. Walleye, smallmouth bass, and largemouth bass predation impacts to age-0 and age-1 yellow perch populations. Age-0 and age-1 yellow perch abundances are based on estimated abundances on June 15th and May 1st, respectively.

	Abundance (#·ha^{-1})		Consumption (#·ha^{-1})				Percent consumed	
Year	Age-0	Age-1	Habitat	Species	Age-0	Age-1	Age-0	Age-1
2007	109,034	117	nearshore	LMB	2,109	75.0	1.9	64.1
				SMB	4,667	33.3	4.3	28.4
				WE	8,003	72.0	7.3	61.5
			offshore	WE	16,816	66.5	15.4	56.8
				TOTAL	31,594	246.7	29.0	210.9
2008	49,178	139	nearshore	LMB	387	87.1	0.8	62.5
				SMB	1,424	5.8	2.9	4.2
				WE	4,232	138.3	8.6	99.3
			offshore	WE	13,061	21.2	26.6	15.2
				TOTAL	19,104	252.4	38.8	181.1
2009	66,340	141	nearshore	LMB	977	46.4	1.5	32.9
				SMB	2,030	37.0	3.1	26.2
				WE	4,507	137.4	6.8	97.4
			offshore	WE	20,523	59.0	30.9	41.8
				TOTAL	28,037	225.6	42.3	198.3

perch in all years (Table 1.4). All three predators consumed a higher number of age-0 yellow perch than age-1 yellow perch.

DISCUSSION

Competitive interactions between predators

Walleye, smallmouth bass, and largemouth bass in Oneida Lake consistently overlap in both time and space and show substantial dietary overlap. All species focus consumption on the most abundant forage species in the lake, including age-0 and age-1 yellow perch, age-0 gizzard shad, and crayfish. Despite this dietary overlap, growth rates for all predators are high which suggests negative impacts from competition for shared resources are limited. Black bass growth rates are similar to fast growing populations of black bass in New York State (Green *et al.* 1986), while walleye growth rates have not declined in recent decades in Oneida Lake (He *et al.* 2005) despite increasing abundances of smallmouth bass and largemouth bass (Irwin *et al.* in press). Walleye growth is relatively slow in Oneida Lake compared to other New York lakes. This is likely due to intraspecific competition for yellow perch (Rudstam *et al.* 1996) and not interspecific competition because black bass consume much less yellow perch than walleye. The lack of population-level consequence is likely due to the ability of all three species to use diverse resources, and is consistent with results from other systems (Fedoruk 1966; Fayram *et al.* 2005; Wuellner *et al.* 2010; Wuellner *et al.* 2011).

When present, negative interactions among walleye and black bass are expected to be via exploitative competition or direct predation on each other, and are

most likely to occur during years with low prey abundance. In Oneida Lake, the timing and extent of offshore walleye foraging during early summer, when age-0 yellow perch are small and abundant offshore, allows offshore walleye to have a disproportionate numerical effect on age-0 yellow perch population dynamics. This should reduce the access of black bass to this dominant prey species later in the season and reduce growth rates, but does not. In Oneida Lake, predator species are able to use multiple forage species within the lake and total consumption is not dependent on availability of age-0 yellow perch (Table 1.3). Therefore, walleye consumption may reduce the ability of black bass to consume age-0 yellow perch, but it does not reduce their ability to consume other prey species in the lake. As a result, the total forage community meets the consumptive demands of all predators and is not determined by age-0 yellow perch year class strength. In other systems with limited forage availability, competition between these predators could be more intense. As black bass continue to expand their northern range into systems with lower species diversity, competition with native predators and black bass may increase in intensity and lead to negative population-level consequences for walleye and other native predators (*e.g.,* Vander Zanden *et al.* 1999).

Seasonal consumption dynamics of predators may lead to negative population consequences through cannibalism and intraguild predation during late summer and fall. Previous research in Oneida Lake has shown that strong year-classes of yellow perch and gizzard shad can buffer other age-classes and species from predation and increase recruitment (Forney 1974; Forney 1977a; Fitzgerald *et al.* 2006). In this study, all predators utilized a greater diversity of prey species in 2008 when age-0

yellow perch densities were low, and included consumption of age-0 walleye and smallmouth bass. Therefore, the intensity of offshore walleye predation on age-0 yellow perch may increase cannibalism and intraguild predation if offshore walleye consumption decreases the abundance of age-0 yellow perch in the nearshore. Further elucidation of the population-level effects of cannibalism and intraguild predation is difficult because of the inconsistent nature of these rare predation events.

Within Oneida Lake, environmental conditions appear to be favorable for both black bass. Prior to age-5, both species exhibited growth rates similar to fast growing bass populations in other lakes in New York State, indicating favorable environmental conditions, such as temperature, available forage, and habitat quality (Green *et al.* 1986). However, growth rates of both black bass species declined after age-5 to rates below slow growing populations in New York State (Green *et al.* 1986). This decrease in growth rates at older age classes may be driven by the forage fish community in Oneida Lake, which tends to be dominated by relatively small, spiny-rayed prey fish. Large, soft-rayed prey fish are present but are limited to age-0 gizzard shad in the fall. As black bass age, access to larger, soft-rayed prey items are limited and likely decreases growth rates in the older fish. Interestingly, decreasing winter severity associated with climate change may increase over-winter survival of age-0 gizzard shad (Fetzer *et al.* 2011) and alewife (Lepak and Kraft 2008), and provide an additional, large prey resource to maintain fast growth rates of smallmouth bass and largemouth bass beyond age-5.

Environmental conditions in Oneida Lake were favorable for smallmouth bass prior to recent ecological changes associated with dreissenid mussel introductions.

Growth rates in this study are nearly identical to those observed during the 1960s (Forney 1972). My *a priori* prediction was that faster growth rates would be observed with increased water temperatures (Jackson *et al.* 2008), water clarity, and areal coverage of littoral habitats (Zhu *et al.* 2006). These conditions should have made the lake more favorable to smallmouth bass (Chu *et al.* 2006). Smallmouth bass may begin to exhibit density-dependent growth with increased abundances, but I suspect that intraspecific competition is low at the current population size. Largemouth bass were historically rare in Oneida Lake (J.L. Forney *personal communication*), limiting the potential to evaluate interactions between largemouth abundance and growth. It is clear that abundance has increased, which is likely related to more favorable environmental conditions, such as increased water clarity and the expansion of the littoral zone (Zhu *et al.* 2006).

Yellow perch population dynamics

Historically, research on consumption of yellow perch in Oneida Lake was primarily limited to studying a single predator, such as walleye (Forney 1977b; Lantry *et al.* 2008), yellow perch (Tarby 1974), and Double-crested Cormorants (*Phalacrocorax auritus*; VanDeValk *et al.* 2002). These studies assumed that all age classes of yellow perch were one well-mixed population. As environmental conditions and the fish community in the lake changed over time, determining predator-prey dynamics and habitat use by fish became increasingly complex. To overcome this complexity, we employed an approach that addresses foraging by diverse predators on multiple life history stages of prey fish in both nearshore and

offshore habitats. In the current study, walleye, smallmouth bass, and largemouth bass were all important predators on age-0 and age-1 yellow perch, but the relative importance of each predator varied across yellow perch life history stage and across habitats. Larval yellow perch consumption was primarily driven by walleye in offshore habitats, while juvenile and age-1 yellow perch consumption was dominated by nearshore walleye, smallmouth bass, and largemouth bass. Though the importance of offshore walleye predation on age-0 yellow perch was documented in the 1970s (Forney 1977b), little was known about the importance of predator consumption in the littoral habitats and their effect on lake-wide population dynamics.

Walleye are the dominant predators of age-0 yellow perch across both habitats, and their effect on age-0 yellow perch was disproportionately high relative to their abundance. In Oneida Lake, walleye are approximately two to five times as abundant as smallmouth bass and largemouth bass but they consume on average 8.5 times and 14 times as many age-0 yellow perch, respectively (range 5 – 45 times as many). The disproportionate effect of walleye is primarily driven by the timing of their age-0 yellow perch consumption, which occurs in the offshore in early summer when age-0 yellow perch are small, abundant, and highly vulnerable. This is also the time when the majority of the walleye population is offshore. As a result, offshore walleye are able to consume many more age-0 yellow perch per day than nearshore walleye, smallmouth bass, and largemouth bass, which consume age-0 yellow perch as juveniles when yellow perch are larger and less abundant. Continued population growth of black bass is not expected to increase the relative importance of these predators substantially since it is unlikely population growth will be large enough to

offset the difference between black bass and walleye numerical consumption of age-0 yellow perch. Additionally, uncertainty associated with black bass abundances should have little effect on my ability to make comparisons between species. Black bass would have to be several times more abundant than walleye to have a similar effect on yellow perch population dynamics. To date, all sampling indicates that this is not the case.

Across all predators, consumption of age-0 yellow perch was highest during 2007, when the yellow perch year-class was the largest. The proportion of mortality that could be attributed to walleye, smallmouth bass, and largemouth bass was the lowest. This suggests that the importance and number of alternative predators, which were not sampled in this study, increases during years with strong year-classes of yellow perch. In all years, my inability to account for age-0 yellow perch mortality with walleye and black bass predation was highest in early summer. By late summer, most observed mortality was accounted for by these three species.

Early mortality of yellow perch has increased in Oneida Lake since the 1990s (Irwin *et al.* 2009) and could be explained by an increasing abundance or efficiency of a predator that was less important in the past. White perch are a likely candidate species because large numbers of larval yellow perch are commonly observed in white perch diets collected through the CBFS long-term gillnet surveys during early summer (Chapter 2). White perch catches in the gillnet survey have increased over the last 30 years (Jackson *et al.* 2012), and their ability to capture larval yellow perch may have increased. If adult (age-3+) white perch densities are similar to yellow perch (Jackson *et al.* 2012), white perch would need to consume between 20 (low abundance: 2008)

and 100 (high abundance: 2007) age-0 yellow perch per night to account for the peak in the difference between observed mortality and consumption estimates during early summer. These numbers are not outside the range of larval yellow perch commonly observed in white perch diets collected through the CBFS long-term gillnet survey. I suspect predation by white perch and other species likely explains the large differences between observed mortality and consumption estimates during early summer and that predation intensity increases during years with stronger age-0 yellow perch year-classes.

Despite lower numerical consumption of age-0 yellow perch by nearshore walleye, smallmouth bass, and largemouth bass relative to offshore walleye, consumption in nearshore habitats is still an important component of yellow perch population dynamics. As limnetic mortality has increased over time and densities in demersal habitats have declined during mid-summer through fall (Irwin *et al.* 2009), age-0 yellow perch population dynamics have become increasingly driven by nearshore habitats, especially during years with weak year-classes. Historically, less than 20% of the age-0 yellow perch production was in nearshore habitats during mid-summer. Currently, 30-70% of the yellow perch production is in nearshore habitats (Chapter 3). Biomass of age-0 yellow perch consumed in littoral habitats was higher in all years investigated because nearshore predators tend to consume larger age-0 yellow perch. Thus, despite lower numbers of yellow perch consumed in littoral habitats, a greater proportion of age-0 yellow perch production is used in the nearshore than in the offshore area. Clearly, littoral yellow perch dynamics are an important component of lake-wide population dynamics.

High consumption of yellow perch by black bass and walleye is not limited to their first year of life but continues throughout their second growing season, and likely plays an important role in determining the number of yellow perch that recruit into the fishery (Nielsen 1980). Large age-0 yellow perch year classes do not appear to buffer age-1 yellow perch from predation, as consumption estimates were similar in all years despite large differences in age-0 abundance across years. The lack of buffering effect is likely due to the timing of predator consumption. During June and July, age-1 yellow perch are likely the most abundant prey fish in littoral habitats since age-0 yellow perch are still primarily limnetic and occupy offshore habitats of the lake and other prey fish are too small to be consumed by predators. Therefore, age-0 yellow perch do not overlap in time or space with age-1 yellow perch during early summer. In contrast to the 1970s (Nielsen 1980), age-0 yellow perch are less of a buffer from predation for age-1 yellow perch regardless of their year class strength.

Impacts of walleye, smallmouth bass, and largemouth bass consumption appears to be the primary source of age-1 yellow perch mortality, since consumption estimates were consistently higher than the number of age-1 yellow perch estimated in the lake at the start of the growing season. This discrepancy suggests that trawling is likely underestimating abundance of age-1 yellow perch during the spring survey. The spring trawling survey is conducted at the beginning of May in habitats greater than 6 m in depth. It is possible that densities of age-1 yellow perch are higher in the nearshore at this time. Limited early summer seine surveys provide some evidence that densities of age-1 yellow perch are much higher in littoral habitats than demersal habitats sampled by the trawl survey (W.W. Fetzer *unpublished data*). This

underestimate may have increased over time as increases in water clarity have increased the extent of macrophytes in littoral habitats (Zhu *et al.* 2006) and distributions of fish in the lake have shifted in response to these changes. However, estimating this trend is difficult given the inconsistent catch patterns of age-1 yellow perch in offshore habitats.

Overestimation of the consumption of age-1 yellow perch could also be the result of variable growth rates of predators across the growing season. In this analysis, I assumed predator growth rates over time were determined from the bioenergetics model using a constant proportion of maximum consumption rate. This is not always true (Lantry *et al.* 2008). If predator growth rates are lower during times when they are consuming age-1 yellow perch, bioenergetics simulations overestimate age-1 perch consumption. Finally, diet estimates in this study were of necessity limited in space and diets of these predators could be different in other areas of the lake.

Regardless of these potential sources of error, nearshore walleye, smallmouth bass, and largemouth bass are likely to have a strong influence on age-1 yellow perch dynamics, and could explain the lack of recovery by the adult yellow perch population following cormorant hazing on Oneida Lake during the 2000s. Previous research indicated that cormorants were a significant source of sub-adult mortality for yellow perch in Oneida Lake (VanDeValk *et al.* 2002). Cormorant hazing by USDA-APHIS has reduced cormorant populations, but sub-adult mortality remains high and yellow perch populations have shown limited recovery (Jackson *et al.* 2012). These results provide evidence that predation by nearshore predators may have replaced predation by cormorant and could be contributing to the lack of recovery by the yellow perch

population. This highlights the importance of monitoring multiple habitats and predator species when assessing sources of mortality. As the relative importance of black bass continues to increase in north temperate lakes, it will be important to understand how predator-prey dynamics change over time and space and how those changes affect population dynamics of ecologically and economically important prey species.

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CHAPTER 2

TEMPORAL TRENDS IN NICHE OVERLAP OF YELLOW PERCH AND WHITE PERCH: IS A PERCH A PERCH?

ABSTRACT

Yellow perch (*Perca flavescens*) and white perch (*Morone americana*) are common generalist predators throughout the Great Lakes basin that can affect the structure of lake ecosystems. Here, I compare habitat use and foraging by yellow perch and white perch in Oneida Lake, New York, USA, using a standardized gillnet survey during periods of low (1975-1987) and high (1997-2008) water clarity. Yellow perch exhibited no changes in their spatial distributions, but evenness of white perch catch across gillnet sites increased during high water clarity. Dietary overlap was high throughout, as consumption of zooplankton was common during both time periods and both species foraged more extensively on benthic macroinvertebrates during periods of high water clarity. Piscivory by yellow perch was dominated by cannibalism, but declined as water clarity increased. White perch consumed age-0 yellow perch early in the growing season but transitioned to consuming age-0 gizzard shad (*Dorosoma cepedianum*) and emerald shiners (*Notropis atherinioides*) by the fall. Spatial, temporal, and dietary overlap tended to be greatest during high water clarity, suggesting greater potential for competition between yellow perch and white perch with increasing water clarity. However, growth rates for both species were similar and did not change across time periods, indicating that pelagic and benthic resources

currently meet the resource requirements of both species and that water clarity did not affect the intensity of competition at current densities.

INTRODUCTION

Yellow perch (*Perca flavescens*) and white perch (*Morone americana*) are intermediate predators common to many north temperature lakes. They occupy a very similar niche, consuming zooplankton, benthic invertebrates, and fish. In northern inland lakes, yellow perch are often native while white perch have been spreading throughout the Great Lakes basin via the canal systems beginning in the 1950's (Dence 1952; Boileau 1985). Both species are ecologically and economically important and a great deal of research has focused on their foraging dynamics, both separately and in systems where they co-occur. Both species undergo similar ontogenetic niche shifts, initially consuming zooplankton and later transitioning to benthic invertebrates (such as chironomids, mayflies, and amphipods) during the juvenile life stage (Elrod *et al.* 1981; Bath and O'Connor 1985; Prout *et al.* 1990; Pelham *et al.* 2001). As adults, piscivory increases in both species, but benthic invertebrates and zooplankton continue to be important diet items (Elrod *et al.* 1981; Parrish and Margraf 1990; Danehy *et al.* 1991; Mayer *et al.* 2001; Truemper et al. 2006; Duncan *et al.* 2011). The relative importance of each diet item can differ across systems and seasons for both species.

Parrish and Margraf (1990) suggested yellow perch are primarily benthivores while white perch are planktivores, though these classifications are often broad and vary seasonally (Elrod *et al.* 1981; Parrish and Margraf 1990; Danehy *et al.* 1991).

Carbon stable isotopes, which provide a long-term integrator of foraging dynamics, also indicate differences in energy pathways leading to yellow perch and white perch foraging across systems. In some lakes, yellow perch and white perch appear to use very similar energy pathways (Bay of Quinte and Lake Erie; Bowman 2005; Campell *et al.* 2009; Guzzo *et al.* 2011), while in others, they do not (Oneida Lake; Bowman 2005). In systems where carbon isotopic signatures differ, yellow perch tend to be more benthivorous.

Piscivory differs between yellow perch and white perch and shows seasonal difference across systems. Yellow perch piscivory increases with size, and can make an important contribution to total lake-wide fish consumption (Tarby 1974; Liao *et al.* 2004). Yellow perch tend to consume age-0 fish later in the growing season (Tarby 1974; Chabot and Maly 1986; Parrish and Margraf 1990; Danehy *et al.* 1991; Truemper *et al.* 2006; Duncan *et al.* 2011), but consumption of age-1 fish can be important in late spring and early summer (Danehy *et al.* 1991). Predation on multiple species is common in yellow perch (Elrod *et al.* 1981; Truemper *et al.* 2006; Carreon-Martinez *et al.* 2011), including cannibalism in late summer (Tarby 1974; Liao *et al.* 2004; Truemper *et al.* 2006).

Piscivory is not as well understood for white perch and appears to be less common. Similar to yellow perch, white perch piscivory increases with size (Elrod *et al.* 1981). Seasonal patterns are inconsistent across systems, and piscivory can be highest in late spring (Bath and O'Connor 1985), late summer/fall (Elrod *et al.* 1981), or spread throughout the growing season (Couture and Watzin 2008). Within a sampling date, white perch consumption of fish tends to be dominated by only a few

species (Carreon-Martinez *et al.* 2011). Seasonal inconsistencies and consumption of only a few species at a time suggest white perch piscivory is opportunistic, taking advantage of prey fish when available (Danehy *et al.* 1991).

Nitrogen stable isotopes indicate species- and system-specific differences in piscivory between yellow perch and white perch. Interestingly, yellow perch are more piscivorous in some lakes (Lake Erie; Campell *et al.* 2009); while white perch are more piscivorous in others (Bay of Quinte and Oneida Lake; Bowman 2005). This inconsistency between yellow perch and white perch diet analysis and nitrogen stable isotopes may be due to difficulties associated with assessing white perch piscivory via diet analyses. If white perch tend to feed on larvae and smaller fish that digest quickly, they could be difficult to detect in traditional diet studies (Legler *et al.* 2010). Combined, these studies suggests yellow perch and white perch foraging dynamics are similar, but species-specific differences may occur due to effects of environmental conditions on prey availability, and subsequently, foraging.

Differences across systems in yellow perch and white perch foraging behavior may be driven by species-specific differences in foraging related to water clarity. Water clarity is a fundamental driver of aquatic ecosystem structure, influencing distributions of habitats (Zhu *et al.* 2006), relative importance of benthic and pelagic energy pathways (Vadeboncoeur *et al.* 2008), and trophic dynamics, such as predator-prey interactions (Lehtiniemi *et al.* 2005; Boscarino *et al.* 2010). The arrival of dreissenid mussels (zebra mussels (*Dreissena polymorpha*) and quagga mussels (*Dreissena rostriformis bugensis*)) and nutrient reductions have resulted in widespread changes in water clarity over the past 25 years in many north temperature ecosystems

where yellow perch and white perch interact (Vanderploeg *et al.* 2002; Dobiesz and Lester 2009). Greater light penetration and benthic-pelagic coupling through dreissenid mussel pseudofeces deposition have elevated the importance of benthic energy pathways in supporting secondary production in these systems through decreases in phytoplankton and zooplankton production and increases in benthic algal, macrophyte, and zoobenthos production (Mills *et al.* 2003; Zhu *et al.* 2006; Higgins and Vander Zanden 2010). In Oneida Lake, New York, adult yellow perch foraging has been influenced by water clarity changes associated with dreissenid introductions, showing positive correlations between water clarity and consumption of benthic prey. Consumption of zooplankton was positively correlated to zooplankton size and not water clarity (Mayer *et al.* 2000). Water clarity also influences sensory capacities of predators and prey. Differences in the response rate of predators and prey to changes in water clarity can favor either the predator or prey, influencing predator-prey dynamics. Further understanding of the relationships between yellow perch and white perch foraging and water clarity is needed to explain observed discrepancies across systems.

Comparisons of yellow perch and white perch foraging across systems or time periods differing in environmental conditions are lacking in the literature, as nearly all studies are limited to several years. Here, I take advantage of a long-term gillnet survey (1975-2008) available for Oneida Lake to evaluate water clarity effects (low: 1975-1987; high: 1997-2008) on yellow perch and white perch: 1) spatial distributions, 2) seasonal foraging dynamics on zooplankton and benthic invertebrates, 3) seasonal patterns of piscivory, and 4) growth rates. Impacts of water clarity on

competitive interactions between similar species are discussed in relation to seasonal foraging dynamics and growth.

METHODS

Study Site

Oneida Lake, New York is a large, shallow lake (area 207 km^2, maximum depth 16.6 m, mean depth 6.5 m) located in the fertile plain of Lake Ontario, and is the site of a long-term monitoring program conducted by the Cornell Biological Field Station. During ice-free months, the lake is well mixed and isothermal, though periods of stratification and hypolimnetic anoxia occurs in some years. Over the past 30 years, several ecosystem perturbations have altered Oneida Lake's food web, including decreases in nutrient loading (Fitzgerald *et al.* in press), changes in the fish community (Irwin *et al.* in press), establishment of Double-crested Cormorants (*Phalacrocorax auritus*; Rudstam *et al.* 2004), and the introduction of dreissenid mussels (Zhu *et al.* 2006). These perturbations lead to reductions in chlorophyll *a*, increases in secchi depth, an expansion of the littoral zone, and a shift from pelagic to benthic primary production (*i.e.* "benthification"; Zhu *et al.* 2006). Zooplankton biomass and production were unchanged and species composition initially shifted from *Daphnia pulicaria* to *Daphnia mendotae* dominance (Idrisi *et al.* 2001), but has since shifted between these two species several times (Cáceres *et al.* in press). Biomass of grazing benthic invertebrates increased following the dreissenid mussel introductions (e.g. Amphipoda and Gastropoda; Mayer *et al.* 2002). The fish community contains over 80 species, but is dominated by warm water species. Yellow

perch are native to the lake; however, white perch are non-native and were first observed in the lake during the mid-1950s (Forney 1980). It is suspected that white perch immigrated up through the Hudson-Mohawk Rivers and entered the lake via the Erie Canal (Aslop and Forney 1962; Boileau 1985).

Gillnet Survey

The Oneida Lake fish community has been monitored for over 50 years using a variety of gears selected primarily to track percids (walleye (*Sander vitreus*) and yellow perch) and other species across multiple life history stages (Forney 1980). A standardized gillnet survey monitors adult fish populations in the lake, providing a relative abundance index for yellow perch and white perch, as well as other species (Rudstam and Jackson 2012). A variable mesh multifilament gillnet was fished overnight at a standard site each week for 15 consecutive weeks starting in the beginning of June and continuing through mid-September (Table 2.1; Figure 2.1). Sites changed each week and were broadly classified into two broad habitat categories: Shoal sites were associated with drop offs and tended to occur near hard substrates (cobble and gravel), while open sites were flat and tended to occur near soft substrates (mud, silt, and organic). The net consisted of four gangs 45.75 m long by 1.83 m deep sewn together to form one 183 m long net. Each gang consisted of six 7.6 m panels with 38, 51, 64, 76, 89 and 102 mm stretch mesh. The net was set around sunset, fished on the bottom, and retrieved in the morning at about 07:30. The time fished varied somewhat with season but was identical for each location each year. All fish (catches of over 60 individuals of a species were subsampled) were measured

Table 2.1. Site- and species-specific catch rates across environmental conditions. Catch rates (± 1 coefficient of variation (SE/mean)) for yellow perch and white perch across low (1975-1987) and high (1997-2008) water clarity for 15 sites sampled through the CBFS long-term gillnet survey. Significant changes (a = 0.05) in the site-specific catch rates indicated in bold. Available: (http://knb.ecoinformatics.org/knb/metacat/kgordon.14.88/knb)

				Yellow Perch		White Perch	
Week	Site	Depth (m)	Site Type	Low	High	Low	High
1	Phillips Point	6.0	Open	169.2 (0.83)	**35.2 (1.24)**	4.5 (1.33)	11.9 (1.07)
2	Dakin Shoal	2.3-7.0	Shoal	110.0 (0.70)	**15.9 (0.98)**	114.5 (0.86)	101.3 (0.56)
3	Shackelton Point	8.6	Open	174.3 (0.46)	**59.2 (0.50)**	2.84 (1.19)	**10.5 (1.04)**
4	Buoy 125	3.0-6.6	Shoal	115.5 (0.59)	**46.0 (0.93)**	148.0 (0.81)	**48.9 (1.39)**
5	Damon Point	9.3	Open	187.5 (0.56)	**60 (0.62)**	6.0 (0.95)	5.3 (1.08)
6	Dutchman Island	4.6-6.6	Shoal	226.9 (0.42)	**60.1 (0.54)**	22.2 (1.13)	19.6 (1.16)
7	Buoy 129	10.0	Open	80.5 (0.49)	**41.8 (0.81)**	2.7 (1.93)	4.91 (1.44)
8	Buoy 113	3.3-8.6	Shoal	91.7 (1.38)	103.1 (0.58)	135.8 (1.06)	**31.8 (0.53)**
9	Cleveland	4.0-7.0	Shoal	80.3 (1.06)	115 (0.49)	0.7 (1.37)	**21.75 (0.84)**
10	Jewell	5.6-12.6	Open	94.4 (0.62)	**43.5 (0.67)**	19.5 (1.00)	31.8 (0.79)
11	Buoy 133	3.3-6.6	Shoal	72.3 (0.59)	**34.8 (0.80)**	8.6 (0.94)	**29.6 (0.94)**
12	Lewis Point	4.0-6.3	Shoal	41.3 (0.80)	**18.1 (0.69)**	13.9 (1.18)	22.0 (1.47)
13	Dunham Island	7.0	Open	33.6 (0.77)	**10.1 (0.94)**	2.15 (1.90)	8.91 (1.18)
14	Willard Island	3.3-10	Shoal	26.3 (1.24)	7.9 (0.61)	4.5 (2.24)	**35.2 (1.14)**
15	Bushnell Point	5.0-9.3	Open	14.5 (0.61)	20.3 (0.80)	6.46 (2.85)	**32.5 (1.05)**

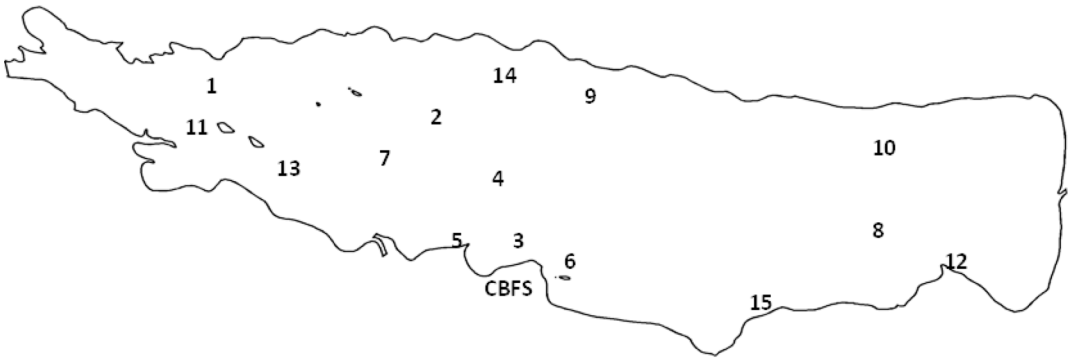

Figure 2.1. Location of 15 gillnets sites within Oneida Lake. Location of gillnet sites in Oneida Lake indicated with numerical values that correspond to sampling week (See Table 2.1 for site details). Location of Cornell Biological Field Station indicated with CBFS.

(total length in mm), weighed (g), sexed, stomach contents recorded, and scales taken for aging. Stomach contents were identified to broad taxonomic categories (*e.g.,* zooplankton, amphipods, fish, chironomids, Trichopterans, and isopods), and if possible, fish observed in stomach contents were identified to species and enumerated.

Analyses were limited to a subset of years within the broader dataset that corresponded to two distinct environmental conditions: low (1975-1987) and high water clarity (1997-2008). Years prior to 1975 were excluded from the analyses because adult white perch populations were not abundant in the lake. Data collected during 1988 through 1996 were also excluded. During this time period, the adult white perch population was low following a disease outbreak in the late 1980s (Irwin *et al.* in press) and water clarity was transitioning from low to high following the introduction of dreissenid mussels (Idrisi *et al.* 2001).

Spatial distributions

Habitat use by yellow perch and white perch during periods of low and high water clarity was determined by the distribution of the total annual catch in the gillnet survey across individual sites. Simpson's index of evenness (*E*) was used to determine patterns of site use by each species and provided a precise, unbiased estimate of evenness that can be used to evaluate whether the total annual catch was dispersed across sites or aggregated on a few sites (Payne *et al.* 2005). Simpson's index of evenness was calculated annually for each species using the equation:

$$E_{1/\hat{D}} = \frac{1/\hat{D}}{s}$$

Where $\hat{D} = \sum p_i^2$ and p_i = proportion of total annual catch captured at site *i*, and *s* = number of sites in the sample. Index values near 0 indicate a patchy distribution, while index values near 1 indicate an even distribution across sites. A Student's t-test was used to compare Simpson's index of evenness during low and high water clarity for each species.

To explain changes in the distribution of the annual catch across individual sites, average catches at each site were compared during low and high water clarity for each species using a Student's t-test. These analyses were used to identify specific sites where catch rates had changed.

Foraging patterns

Diet data from the gillnet survey were used to calculate frequency of occurrence of major diet items for yellow perch and white perch. For each species, frequency of occurrence was calculated only for each sampling event when 10 or more diets were collected to avoid overrepresentation of sampling dates when only a few fish were caught. Fish with empty stomachs were not included in calculation of frequency of occurrence. Major taxonomic groups analyzed were zooplankton, amphipods, fish, chironomids, Trichopterans, and isopods. Less common diet items were clustered into a separate "other" category. In addition to the broad fish category, frequency of occurrence was also determined for the most common fish species present in the diets, including age-0 yellow perch, age-0 gizzard shad (*Dorosoma cepedianum*), emerald shiners (*Notropis atherinioides*), tessellated darters (*Etheostoma olmstedi*), and white perch.

Logistic regression was used to test for differences in seasonal foraging patterns between yellow perch and white perch during low and high water clarity in the lake. A set of all potential candidate models was developed using month, trophic state, species, and their potential interactions. Month was treated as a continuous predictor, with each month assigned ascending numerical values (e.g. June = 1, July = 2, and so on). The seasonal trends in the availability of different diet items (e.g., *Daphnia spp.* and age-0 fish) tend to decrease or increase over time, and should influence their importance in yellow perch and white perch diets. Across all diet items, the best-fitting, most parsimonious model was selected using Akaike's Information Criterion (AIC; Burnham and Anderson 2002).

In addition to individual diet items, Pianka's Index (O) was calculated to compare total dietary overlap between yellow perch and white perch on dates when both species had 10 or more diets collected. Though other overlap indices can produce less biased estimates (Linton *et al.* 1981), my analyses were limited to Pianka's Index because available data was in frequency of occurrence and not percent by weight. Pianka's Index was calculated using the following equation:

$$O = \frac{\sum_{i=1}^{n} \left(p_{ji} \cdot p_{ki} \right)}{\sqrt{\left(\sum_{i=1}^{n} p_{ji}^2 \sum_{i=1}^{n} p_{ki}^2 \right)}}$$

Where p_{ji} and p_{ki} are proportions of the resource i used by species j and k, respectively (Pianka 1974). Index values near 0 indicate complete separation, while index values near 1 indicate total overlap. Diet overlap was compared during low and high water

clarity using multiple regression and Akaike's Information Criterion (Burnham and Anderson 2002).

Growth rate comparisons

Yellow perch and white perch ages were determined with scales collected in the gillnet survey and used to test for differences in growth patterns during low and high water clarity and across species. Von Bertalanffy growth curves were fit to the average length-at-age for each species using all available data and separately using only data from each time period. The combined AIC from the models fit within each time period was compared to the AIC from the model using all available data (Burnham and Anderson 2002). If fitting the growth models separately for the two time periods improved the AIC by two or more units, it was concluded that growth patterns were different under low and high water clarity. Differences in growth patterns across species were assessed following a similar protocol by fitting a Von Bertalanffy growth curve to each species individually and then comparing it to a growth curve fit with data from both species using the same AIC selection process.

RESULTS

Spatial distribution

Yellow perch catch-per-unit-effort (CPUE) was significantly higher during low water clarity, declining from 101.8 fish per net night to 44.7 (t-test, $T_{277.5} = 7.4061$, $p < 0.001$). The coefficient of variation was similar during low (0.95) and high (1.00) water clarity. Evenness of yellow perch catch across sites was not different during

low (0.59) and high (0.54) water clarity (t-test, $T_{22.6} = 1.685$, $p = 0.11$; Figure 2.2). Therefore, yellow perch spatial distributions did not change across time periods and was reflected in the site-specific catch rates across time periods, which declined or remained unchanged across all sites (Table 2.1).

White perch CPUE was similar during low and high water clarity (t-test, $T_{296.9} = 0.746$, $p = 0.46$), at 32.2 and 27.7 fish per net night, respectively. The coefficient of variation decreased from 2.27 to 1.37. Evenness of spatial distributions became less aggregated (t-test, $T_{17.59} = 3.62$, $p < 0.01$), shifting from 0.24 to 0.43 (Figure 2.2). During low water clarity, white perch distributions were patchy and three sites dominated total annual catch (Table 2.1; Dakin Shoal, Buoy 125, and Buoy 113). However, during high water clarity catches at two of these three sites declined significantly, while catch rates at five sites increased significantly.

Foraging patterns

Throughout the study, 281 and 154 sampling events had 10 or more diets collected for yellow perch and white perch, respectively. Diets analyzed across all dates totaled 12,526 for yellow perch and 5,518 for white perch. Of these diets, 43% and 32% were empty for yellow perch and white perch, respectively (Table 2.2). Zooplankton, amphipods, fish and chironomids were the most common diet items for both species; however, consumption of these diet items varied seasonally and across species and time periods (Table 2.2, 2.3; Figure 2.3). Both species showed similar seasonal patterns of zooplankton consumption, peaking in early summer and declining throughout the growing season. Frequency of zooplankton occurrence was highest in

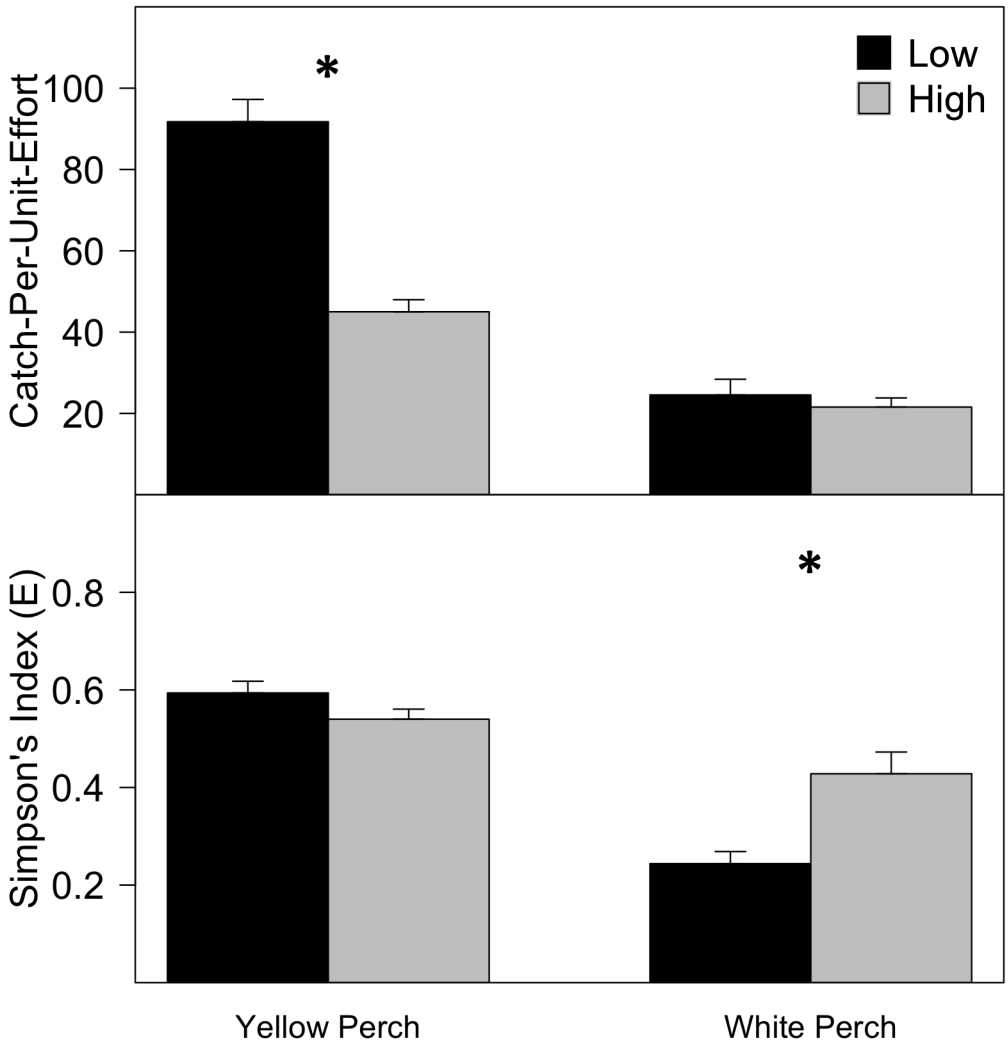

Figure 2.2. Catch-per-unit-effort and Simpson's Index (*E*) for yellow perch and white perch. Mean and 95% confidence interval for catch rates and Simpson's Index (*E*) for yellow perch and white perch during low and high water clarity. Significant differences (a = 0.05) indicated with an asterisk (*).

Table 2.2. Summary table of yellow perch and white perch foraging dynamics. Yellow perch and white perch monthly diet information during low and high water clarity. Dietary information presented as frequency of occurrence of zooplankton (Zoo), amphipods (Amp), fish, chironomids (Chiro), Trichopterans (Tricho), isopods (Iso), and other. Pianka's Index (*O*) expressed as monthly overlap between yellow perch and white perch.

			# Dates			Percent	Pianka's	Frequency of Occurrence						
Species	Water Clarity	Month	≥10 Diets	# Diets	# Empty	Empty	Index (*O*)	Zoo	Amp	Fish	Chiro	Tricho	Iso	Other
Yellow Perch	Low	June	46	2368	793	34.6	0.72	0.51	0.26	0.07	0.23	0.05	0.05	0.13
		July	48	2532	1121	44.5	0.70	0.23	0.42	0.32	0.13	0.03	0.02	0.09
		August	43	1847	989	55.4	0.49	0.20	0.18	0.48	0.17	0.02	0.01	0.06
		September	13	348	22	61.9	0.95	0.10	0.23	0.48	0.06	0.02	0.00	0.11
	High	June	36	1554	567	37.2	0.79	0.52	0.45	0.08	0.10	0.21	0.04	0.13
		July	50	2428	948	39.3	0.68	0.21	0.63	0.08	0.15	0.20	0.01	0.18
		August	36	1247	780	63.8	0.66	0.13	0.31	0.16	0.23	0.11	0.00	0.23
		September	9	202	164	79.7	0.50	0.06	0.12	0.48	0.09	0.00	0.00	0.37
White Perch	Low	June	23	1324	402	30.3	-	0.50	0.26	0.19	0.41	0.02	0.00	0.04
		July	15	561	132	25.1	-	0.19	0.54	0.16	0.46	0.00	0.00	0.03
		August	12	274	46	20.0	-	0.06	0.32	0.35	0.52	0.00	0.00	0.02
		September	3	88	30	36.4	-	0.25	0.42	0.42	0.03	0.00	0.00	0.00
	High	June	33	1258	456	34.1	-	0.34	0.41	0.18	0.26	0.05	0.02	0.13
		July	24	697	221	33.3	-	0.09	0.88	0.07	0.09	0.06	0.00	0.07
		August	28	818	312	37.1	-	0.07	0.75	0.17	0.17	0.10	0.01	0.06
		September	16	498	194	35.1	-	0.04	0.79	0.23	0.11	0.01	0.01	0.02

Table 2.3. Logistic regression model selection and coefficients summary table for frequency of occurrence of major diet items. Logistic model selection results identified with AIC, positive values indicate higher frequency of occurrence. AIC_c, Akaike weights (w_i), and evidence ratios (w_1/w_i) are included only for candidate models with evidence ratios < 10. Best fitting, most parsimonious model indicated with italics; significant model coefficients are indicated in bold. Constants correspond to white perch during high water clarity without a month effect; therefore, coefficients correspond to seasonal trends (Month), yellow perch (YP), and low water clarity (Low).

				Model Coefficient							
Model	ΔAIC_c	w_i	w_1/w_i	Intercept	Month	Low	YP	Month: Low	Month: YP	Low: YP	Month: Low:YP
Zooplankton											
Month x Water clarity x Species	-	1	1	**0.36**	**-1.20**	1.12	**0.63**	-0.19	**0.23**	**1.32**	**0.36**
Amphipod											
Month x Water clarity x Species	-	1	1	**-0.91**	**0.78**	-0.24	**1.24**	**-0.41**	**-0.96**	**-0.66**	**0.50**
Fish											
Month x Water clarity x Species	-	1	1	**-1.76**	0.05	0.05	**-1.51**	**0.18**	**0.33**	-0.04	**0.45**
Chironomid											
Month x Water clarity x Species	-	1	1	**-0.30**	**-0.51**	-0.15	**-2.40**	**0.59**	**1.11**	**2.00**	**-1.48**
Trichoptera											
Month x Water clarity x Species	-	0.98	1	**-2.88**	**0.12**	1.22	**2.28**	**-2.38**	**-0.67**	**3.22**	**2.56**
Isopod											
Month x Water clarity x Species	-	0.65	1	**-4.02**	-0.03	12.67	**1.70**	-13.83	**-0.78**	-11.96	13.55
Water clarity x Species + Month	2.11	0.23	2.87	**-2.86**	**-1.00**	**-1.77**	0.48			**2.13**	
Month x Species	3.66	0.11	6.22	**-4.58**	-0.21		**2.75**		**-1.03**		
Other											
Month x Water clarity x Species	-	1	1	**-1.26**	**-0.59**	**-2.04**	**-0.82**	**0.44**	**0.83**	**1.66**	**-0.70**
Pianka's Index (*O*)											
Month	-	0.81	1	**0.85**	**-0.08**						
Month + Water clarity	1.19	0.16	4.98	**0.83**	**-0.08**	0.04					

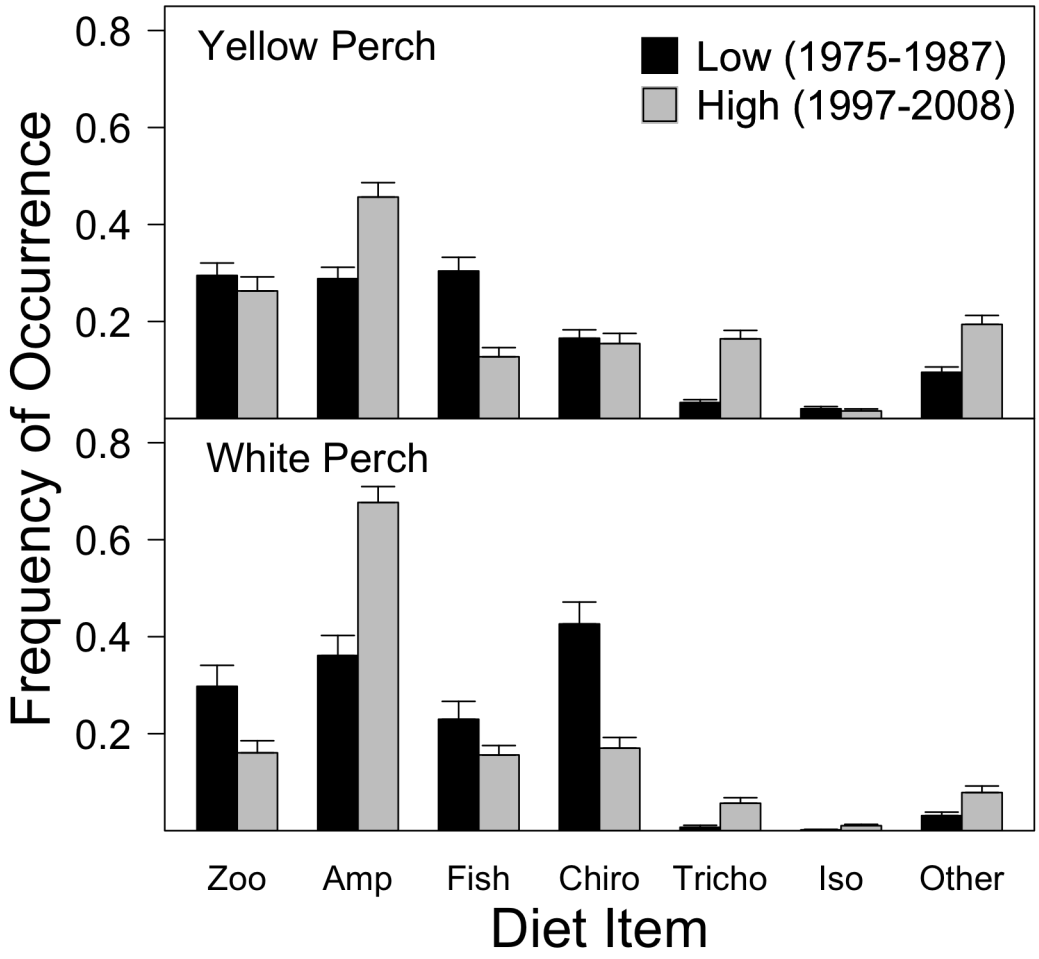

Figure 2.3. Frequency of occurrence for major diet items for yellow perch and white perch. Mean and 95% confidence interval for frequency of occurrence of major diet items observed in yellow perch and white perch stomachs during low and high water clarity. Major diet items include zooplankton (Zoo), amphipods (Amp), fish (Fish), chironomids (Chiro), Trichopterans (Tricho), isopods (Iso), and other prey items (Other).

yellow perch and white perch during low water clarity (Table 2.3). Dynamics of amphipod consumption were more complex with each species exhibiting different seasonal foraging patterns and responses to changing environmental conditions (Figure 2.3). White perch consumption of amphipods increased later in the growing season and was more common during high water clarity. Yellow perch amphipod consumption varied little across the season during low water clarity, but declined over the growing season during high water clarity. Chironomid consumption was highest in white perch, and declined for both species during high water clarity (Figure 2.3). Seasonal trends were inconsistent for both species (Table 2.2, 2.3). Trichopterans consumption was highest in yellow perch and highest for both species during high water clarity (Table 2.2, 2.3; Figure 2.3). Seasonal foraging patterns differed across species and time periods. Consumption of isopods was uncommon for both species, but tended to be higher for yellow perch (Table 2.2, 2.3; Figure 2.3). Consumption of "other" diet items was highest during high water clarity, and tended to increase for yellow perch and decrease for white perch over the growing season (Table 2.2, 2.3; Figure 2.3). Diet items in the "other" category included Hemiptera, Ephemeroptera, zebra mussels, mollusks, crayfish, and leeches.

Frequency of fish in diets was highest for white perch, but showed the greatest difference between time periods for yellow perch. Yellow perch consumption of fish was common during low water clarity and increased over the growing season (Table 2.2, 2.3; Figure 2.4). For both species, age-0 yellow perch were the most frequently consumed fish group (Figure 2.4), followed by age-0 gizzard shad, emerald shiners, tessellated darters and age-0 white perch. Consumption of age-0 yellow perch was

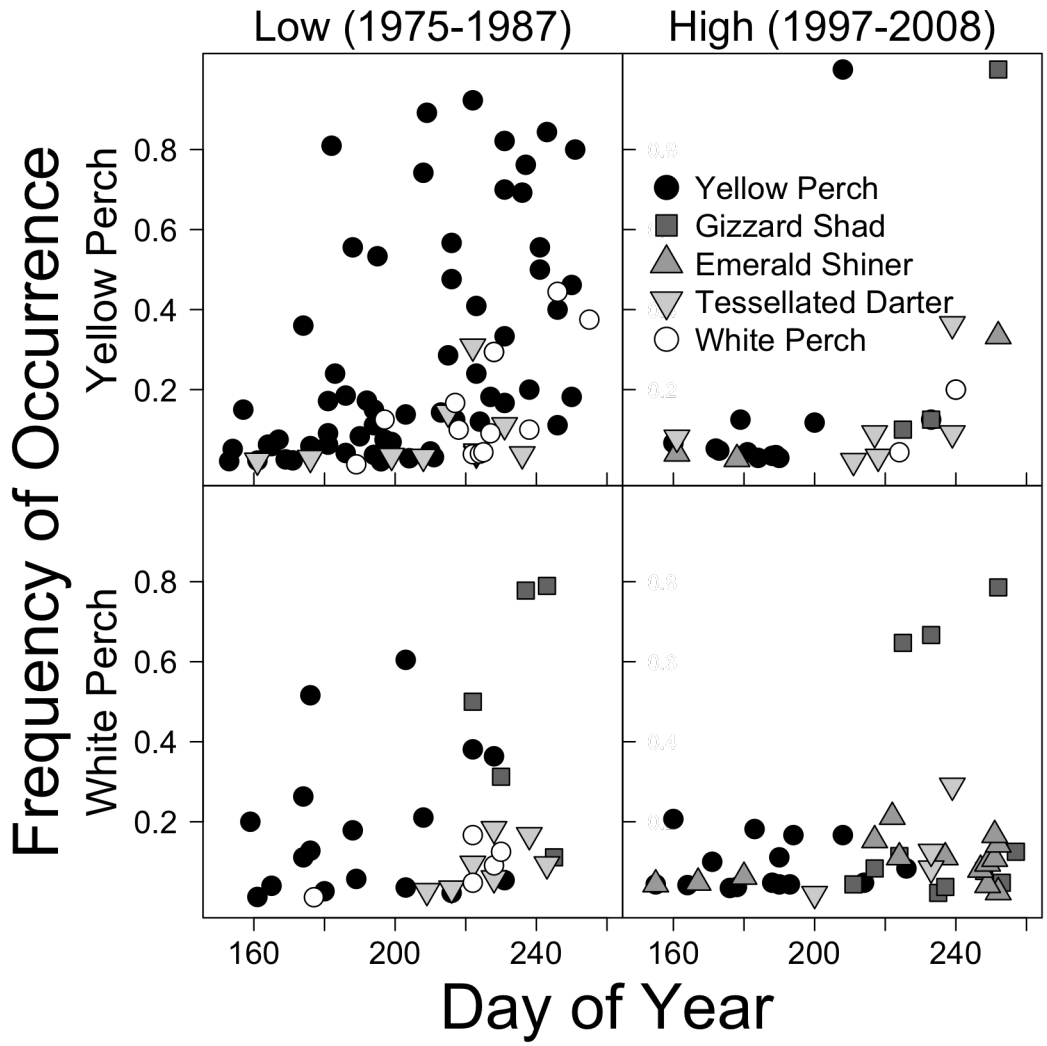

Figure 2.4. Seasonal patterns of fish species in diets of yellow perch and white perch. Frequency of occurrence of major fish species observed in yellow perch and white perch diets during low and high water clarity. Only dates when fish were observed in diets are plotted.

highest during low water clarity. During low water clarity, consumption of age-0 yellow perch increased throughout the summer; however, during high water clarity, consumption was highest during early summer. Consumption of age-0 yellow perch tended to be higher in white perch (Table 2.4; Figure 2.4). Consumption of age-0 gizzard shad and emerald shiner increased later in summer for both species, was higher during high water clarity, and was most common in white perch (Table 2.4; Figure 2.4). Consumption of tessellated darters was not different across species or time periods, but increased over the growing season (Table 2.4; Figure 2.4). White perch were more common in the diets of yellow perch during low water clarity, and increased over the growing season (Table 2.4; Figure 2.4). Other species consumed infrequently included logperch (*Percina caprodes*), *Lepomis spp.* (pumpkinseed (*Lepomis gibbosus*) and bluegill (*Lepomis macrochirus*)), smallmouth bass (*Micropterus dolomieu*), trout-perch (*Percopsis omiscomaycus*), white sucker (*Catostomus commersonii*), and channel catfish (*Ictalurus punctatus*).

Dietary overlap, measured as Pianka's Index (*O*) was high for both time periods, ranging from 0.49 to 0.95. The degree of dietary overlap decreased in late summer; however, the strength of this decline was weak. No changes in dietary overlap were observed across time periods (Table 2.2, 2.3).

Growth rate comparisons

AIC values for yellow perch and white perch were lower when the Von Bertalanffy growth curve was fit for data from both time periods; therefore, growth patterns were not different during low and high water clarity (Table 2.5; Figure 2.5).

Table 2.4. Logistic regression model selection and coefficients summary table for frequency of occurrence of fish in diets. Logistic model selection results identified with AIC, positive coefficient values indicate higher frequency of occurrence. AIC_c, Akaike weights (w_i), and evidence ratios (w_1/w_i) are included only for candidate models with evidence ratios < 10. Best fitting, most parsimonious model indicated with italics; significant model coefficients are indicated in bold. Constants correspond to white perch during high water clarity without a month effect; therefore, coefficients correspond to seasonal trends (Month), yellow perch (YP), and low water clarity (Low).

				Model Coefficient							
Model	ΔAIC_c	w_i	w_1/w_i	Intercept	Month	Low	YP	Month: Low	Month: YP	Low: YP	Month: Low:YP
Yellow Perch											
Month x Water clarity x Species	-	1.00	1.00	**-3.37**	**-0.56**	0.26	**-1.23**	**0.73**	0.42	-0.04	0.41
Gizzard Shad											
Month x Water clarity + Species	-	0.49	1.00	**-6.79**	**1.08**	**-3.34**	**-3.77**	**1.24**			
Month x Water clarity x Species	0.04	0.48	1.02	**-6.76**	**1.05**	**-3.32**	**-6.82**	**1.29**	1.52	-6.65	-3.54
Emerald Shiner											
Month + Water clarity + Species	-	0.71	1.00	**-6.97**	**1.03**	-18.19	**-1.86**				
Month x Species + Water clarity	4.02	0.10	7.45	**-6.94**	**1.03**	-18.20	-2.07		0.08		
Month x Water clarity + Species	4.03	0.09	7.51	**-6.96**	**2.03**	-16.75	**-1.85**	-0.63			
Water clarity x Species + Month	4.03	0.10	7.51	**-6.97**	**1.03**	-19.16	**-1.85**			1.73	
Tessellated Darter											
Month	-	0.45	1.00	**-7.71**	**1.02**						
Month + Species	1.42	0.22	2.04	**-8.22**	**1.09**		0.49				
Month + Water clarity	2.19	0.15	2.99	**-7.99**	**1.05**	0.38					
Month x Species	4.18	0.06	8.07	**-7.55**	**0.09**		-0.55		0.36		
Month x Water clarity	4.24	0.05	8.34	**-7.34**	**0.82**	-0.81		0.43			
White Perch											
Month + Water clarity	-	0.45	1.00	**-11.41**	**1.37**	**3.07**					
Month + Water clarity + Species	1.16	0.25	1.79	**-11.78**	**1.39**	**2.81**	0.72				
Water clarity x Species + Month	2.45	0.13	3.42	-26.60	**1.42**	17.71	16.08			-15.56	
Month x Species + Water clarity	3.73	0.07	6.48	**-10.43**	0.95	-0.89	2.69		**0.56**		
Month x Water clarity	3.90	0.07	7.04	**-10.59**	1.11	2.20		0.28			

Table 2.5. Parameters for Von Bertalanffy growth equation and model selection results. Von Bertalanffy growth equations parameters for yellow perch and white perch fit during different time periods, across both time periods, and with all species combined. Growth parameters include maximum length (L_{inf}), rate constant (k), and x-intercept (t_0). Best fitting, most parsimonious model indicated with AIC = 0.00.

Comparison	Species	Water Clarity	L_{inf}	k	t_0	AIC
Time Period	Yellow Perch	Low	277.51	0.60	-0.03	2.60
		High	292.02	0.50	-0.08	
		All Data	284.26	0.55	-0.05	0.00
	White Perch	Low	288.50	0.62	-0.05	3.10
		High	301.81	0.56	-0.05	
		All Data	295.10	0.59	-0.05	0.00
Species	Yellow Perch	All Data	284.26	0.55	-0.05	0.00
	White Perch	All Data	295.10	0.59	-0.05	
	All	All Data	289.70	0.57	-0.05	5.14

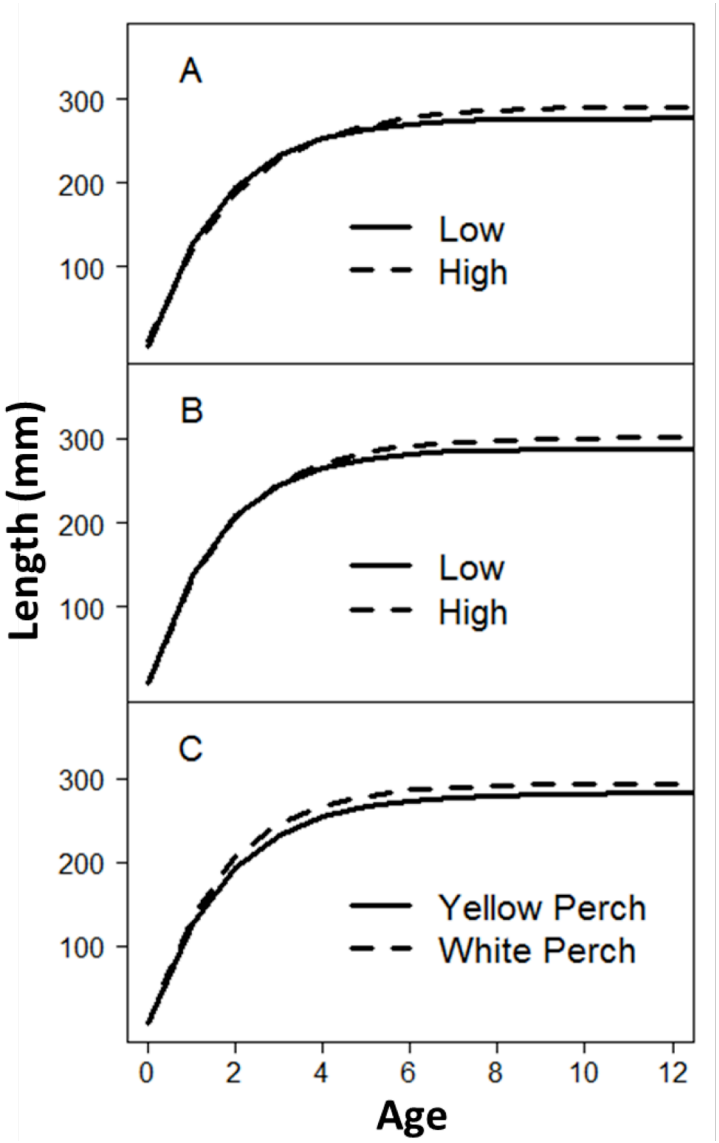

Figure 2.5. Von Bertalanffy growth curves of yellow perch and white perch. Von Bertalanffy growth curves during low and high water clarity for yellow perch (A) and white perch (B). Von Bertalanffy growth curves for each species fit using data from both time periods (C).

Across species, yellow perch and white perch exhibited different growth patterns, with white perch growing faster and larger. The magnitude of these differences was minimal (Table 2.5; Figure 2.5).

DISCUSSION

Spatial distributions

The distribution of yellow perch and white perch catch across gillnet sites differed across species and time periods, and suggests different patterns of habitat use under different water clarity conditions for white perch, but not for yellow perch. Yellow perch catch per night was twice as high during low water clarity. This decrease is likely driven by Double-crested Cormorant consumption of sub-adult yellow perch (Rudstam *et al.* 2004), but increasing mortality rates during earlier life stages may also be important (Irwin *et al.* 2009). The evenness of the distribution across gillnet sites did not change and fish were commonly captured in both open and shoal habitats in Oneida Lake. This supports previous observations that open and shoal habitats are both good habitats for yellow perch (Fish and Savitz 1983; Stang and Hubert 1984; Radabaugh *et al.* 2010) since it would be expected that as abundance decreased, those sites with the most favorable conditions would dominate the catch. Contrary to yellow perch, white perch catch rates did not differ across time periods, but the evenness of their distribution across sites increased at high water clarity. During low water clarity, white perch catch was dominated by shallow, shoal sites that were fished early in the summer, and likely overlapped with spawning congregations at these sites. Catch rates at other sites were consistently low; suggesting white perch

use of demersal habitats was limited. As water clarity increased, white perch became less aggregated and more dispersed across Oneida Lakes habitats, as evident by increases in catch rates at 5 sites and a decline in catch rates at 2 of the 3 sites that were historically dominant. During low water clarity, I suspect white perch were primarily distributed within the pelagic habitats of the lake, limiting the effectiveness of the benthic gillnet survey to capture suspended fish. However, as water clarity increased, I suspect white perch began to use greater depths and benthic habitats, increasing the overlap between their habitat use and the gillnet survey, thereby changing the catchability in the standard net sets.

Differences in the patterns of habitat use by yellow perch and white perch between time periods could help to explain some of the discrepancies in the literature about the general foraging strategies of each species. During both time periods, yellow perch were common across all sites and their habitat use was consistent with their classification as a benthivore (Parrish and Margraf 1990). White perch, however, seemed to exhibit different patterns of habitat use depending on water clarity. During low water clarity, spatial overlap between white perch and the gillnet survey was limited to early summer spawning sites, suggesting white perch were primarily suspended in open water. During high water clarity, white perch catch increased at shoal sites with cobble and gravel substrates throughout the growing season, suggesting a greater use of benthic habitats. These patterns are consistent with the transition from a planktivore to increased benthivory during high water clarity observed in my diet data. Therefore, the degree of habitat overlap and the potential for competitive interactions between species likely varies based on environmental

conditions, and is expected to be more intense during high water clarity if resources are limited.

Foraging dynamics

Yellow perch and white perch exhibited high dietary overlap during both water clarity conditions, as both species tended to rely heavily on both zooplankton and benthic invertebrates. The extent of benthic invertebrate reliance differed between time periods. For both species, foraging appears to be opportunistic and varies based on seasonal patterns of prey availability. Evidence to classify either species as primarily a planktivore or benthivore was limited based on analyses of common diet items, but increased when patterns of piscivory and habitat use were included. Seasonal foraging patterns associated with changes in prey availability are consistent with observations of both species from other systems (Elrod *et al.* 1981; Parrish and Margraf 1990; Danehy *et al.* 1991; Mayer *et al.* 2001; Truemper et al. 2006; Duncan *et al.* 2011). During early to mid-summer when *Daphnia spp.* are abundant in Oneida Lake (Idrisi *et al.* 2001), consumption is dominated by zooplankton, but shifts to amphipods and other benthic invertebrates as zooplankton abundance declines. By late summer, both species frequently consume age-0 fish as their size in the lake increases. Consumption of chironomids, Trichopterans, isopods, and other macroinvertebrates was less common and did not show clear seasonal trends.

Differences in foraging between time periods were less pronounced than expected. Increases in water clarity have been shown to shift the relative importance of energy pathways in lakes from pelagic to benthic production (Higgins and Vander

Zanden 2010), and several studies have demonstrated that this effect transferred up through the food web to fish (Mayer *et al.* 2001; Truemper *et al.* 2006; Chapter 3). In Oneida Lake, zooplankton were an important component of the diets of both species during both water clarity conditions, though some slight declines in their frequency of occurrence were observed. The largest changes in diets were associated with shifts in both species use of benthic macroinvertebrates. Consumption of macroinvertebrates was common for yellow perch during both time periods, but did generally increase during high water clarity, especially for amphipods and Trichopterans. Consumption of other less common benthic macroinvertebrates also increased, including consumption of Hemiptera, Ephemeroptera, dreissenid mussels, mollusks, and crayfish. Similarly, white perch consumption of macroinvertebrates increased during high water clarity, and was dominated by amphipods and Trichopterans. Amphipod consumption by white perch increased the most and became the most frequently observed diet item in all months. Interestingly, amphipod consumption by white perch replaced chironomids as the most common macroinvertebrate consumed by white perch, as chironomid consumption declined for both species during high water clarity. This was likely driven by a decline in chironomids that began prior to dreissenid mussel introductions (Mayer *et al.* 2002).

Shifts towards more consumption of benthic macroinvertebrates during high water clarity and changes in spatial distributions, especially for white perch, provides some evidence to explain differences in niche overlap between these species across different studies (*e.g.,* high overlap: Elrod *et al.* 1981; Danehy *et al.* 1991; low overlap: Parrish and Margraf 1990). My assessment of dietary overlap between

yellow perch and white perch is limited to sampling dates when both species were overlapping in time and space. At those times, the two species consumed similar prey items. However, throughout the majority of the growing season, spatial and temporal overlap of yellow perch and white perch may have been limited, potentially leading to less dietary overlap. As water clarity increased, white perch catch rates shifted to a more even distribution across gillnet sites indicating greater spatial and temporal overlap between white perch and yellow perch. This change in spatial distributions suggests the dietary overlap measured through the gillnet survey likely represents a more realistic picture of the true dietary overlap between these species during high water clarity.

Diet data for either species from open water habitats are unavailable, limiting my ability to explore these patterns further and provide a clearer picture of foraging patterns across all habitats of Oneida Lake. Overall, I suspect that during low water clarity white perch more commonly occupied pelagic habitats and were primarily planktivorous, while yellow perch primarily occupied benthic habitats and relied more heavily on benthic invertebrates. As water clarity increased and primary production shifted from pelagic to benthic habitats, I suspect white perch increasingly occupied benthic habitats and their diet became more benthivorous, increasing their dietary overlap with yellow perch. This hypothesis is consistent with observation from other systems, specifically low overlap in Lake Erie during the late 1980s (low water clarity; Parrish and Margraf 1990) and high overlap in systems with higher water clarity (Elrod *et al.* 1981; Danehy *et al.* 1991).

Patterns of piscivory by yellow perch and white perch provide additional evidence that yellow perch tend to be benthivores while white perch tend to be planktivores. Fish consumed by yellow perch are dominated by juvenile yellow perch and tessellated darters, which tend to occupy demersal habitats. Consumption of pelagic species such as age-0 gizzard shad and emerald shiners was limited. White perch fed primarily on age-0 yellow perch during early summer, when age-0 yellow perch are limnetic (Irwin *et al.* 2009) and transitioned to age-0 gizzard shad and emerald shiners during late summer.

Piscivory by both species was not consistent across time periods. During low water clarity, cannibalism by yellow perch was common during late summer (Tarby 1974), but it was not common during high water clarity. I suspect this decline was driven by reduced abundances of juvenile yellow perch in demersal habitats of Oneida Lake since the late 1980s (Irwin *et al.* 2009). Yellow perch consumption of age-0 white perch has also declined, suggesting that yellow perch currently have a limited effect on white perch recruitment. Yellow perch consumption of age-0 gizzard shad and emerald shiners increased in recent years and was likely driven by increasing abundances of these species (Fitzgerald *et al.* 2006; Irwin *et al.* in press). Overall, the extent and timing of yellow perch piscivory was fairly consistent with observations made in other systems (Tarby 1974; Chabot and Maly 1986; Parrish and Margraf 1990; Danehy *et al.* 1991; Truemper *et al.* 2006; Duncan *et al.* 2011).

White perch consumption of age-0 yellow perch shows less change between time periods, and typically occurs early in summer when age-0 yellow perch are small and highly vulnerable to predation. The lack of change between time periods despite

reduced abundances and the timing of consumption, suggest white perch could account for a greater proportion of early mortality in age-0 yellow perch during high water clarity (Irwin *et al.* 2009). However, assessing the effect of white perch consumption on yellow perch recruitment remains difficult with the data available from the gillnet survey and the lack of adult white perch population estimates available for Oneida Lake. White perch consumption of age-0 gizzard shad and emerald shiners has increased over time, and these species are commonly found in the diets of white perch during late summer and early fall. White perch appear to take advantage of diverse prey species when available, and that could explain why different seasonal patterns of white perch piscivory have been observed across other systems that differ in the seasonal availability of prey species (Elrod *et al.* 1981; Bath and O'Connor 1985; Couture and Watzin 2008).

Interspecific interactions

Over the last 50 years, white perch have increased across the Great Lakes basin while yellow perch have declined (Knight and Vondracek; Hawes and Parrish 2003; Hoyle *et al.* 2012; Irwin *et al.* in press), shifting fish community composition and raising concerns about how this may impact food web dynamics in these systems. Overall, I found strong evidence that yellow perch and white perch occupy similar niches, though the degree of divergence between more benthivory in yellow perch and more planktivory in white perch likely increases in systems with low water clarity. High dietary overlap during both time periods and greater spatial overlap during high water clarity does not appear to result in strong interspecific competition between

yellow perch and white perch. Both species were able to adapt foraging strategies to take advantage of changing prey communities as water clarity increased and they exhibited no changes in their growth rates. In fact, length-at-age curves for both species are very similar, though white perch do grow slightly faster and reach a slightly larger maximum length (L_{inf}). At current and historical abundances for yellow perch and white perch, availability of zooplankton, benthic invertebrates, and fish appears high enough to support both predator species without negative competitive consequences at the adult life stage. Oneida Lake's size and depth likely limit competition because both species have access to both benthic and pelagic resources throughout the growing season as the lake rarely stratifies and hypoxia is uncommon. However, in lakes with less access to both benthic and pelagic energy pathways, competition would be expected to intensify.

Negative interspecific interactions between adult white perch and yellow perch are likely limited to direct predation on young of each species, as both species consumed the other at early life stages. I suspect that white perch likely have a larger effect on recruitment dynamics of other species, specifically yellow perch, because they consume age-0 yellow perch and other fish species during pelagic life stages when they are smaller and more vulnerable to higher predation rates. Yellow perch consumption of white perch was most common during low water clarity, and was rarely observed in recent years. This suggests it is unlikely that adult yellow perch currently impact white perch recruitment dynamics through direct predation or competition, despite competition observed at early life stages (Prout *et al.* 1990). As the populations of these species continue to change, future research should focus on

patterns of piscivory for these two species, and how this varies under different environmental conditions and fish communities.

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CHAPTER 3

INDIVIDUAL SPECIALIZATION PROMOTES RESILIENCE TO CHANGING ECOSYSTEM STATES

ABSTRACT

Populations consist of individuals yet few studies have attempted to integrate how individual specialization influences the energy pathways that support consumer production. Here, I take advantage of multiple long-term data sets and archived samples available for Oneida Lake, New York, to determine spatial and temporal patterns of energy pathways used by age-0 yellow perch (*Perca flavescens*) under eutrophic and mesotrophic conditions. Preserved age-0 yellow perch samples were analyzed from four years during the 1960s (eutrophic) and 2000s (mesotrophic) that differ in age-0 yellow perch density (*i.e.* low and high; 8 years total). Individual fish were analyzed for individual diet and stable isotope ratios of $\delta^{13}C$ and $\delta^{15}N$ to quantify level of specialization. Data were integrated with time series of habitat-specific catch statistics to determine benthic reliance of the total age-0 yellow perch population. Diet and stable isotope analyses demonstrate clear specialization of individuals on either benthic or pelagic resources. Population-level benthic reliance increased from 10-20% in the 1960s to 30-70% in the 2000s. At low densities, a larger proportion of the population resided in littoral habitats, and resulted in a higher reliance on benthic carbon by the total population during both time periods. Results highlight the ability of fish to integrate both benthic and pelagic energy pathways, and provide clear evidence that ecosystem state and population density interact to drive energy pathways

supporting consumer production. I propose that individual specialization within a population stabilizes population dynamics and increases resilience to ecosystem perturbations because individuals within a population are able to take advantage of changing ecological conditions.

INTRODUCTION

Understanding extrinsic and intrinsic drivers of niche breadth and resource use is a central challenge in ecology (Elton 1927; Schoener 1974). In lake ecosystems, where the dominant paradigm has been that fish production is driven by pelagic-phytoplankton-based food chains, there has been growing evidence that benthic (Hecky and Hesslein 1995; Vander Zanden and Vadeboncoeur 2002; Vadeboncoeur *et al.* 2008) and terrestrial energy pathways (Pace *et al.* 2004; Weidel *et al.* 2008; Solomon *et al.* 2011) are also important in supporting production at higher trophic levels. Concurrently, there has been growing recognition that resource use within a population is often highly specialized across individuals (Bolnick *et al.* 2003; Bolnick *et al.* 2007; Svanbäck *et al.* 2008), such that individual niche breadth only represents a subset of the total population niche. Despite overlap between these two research areas, few studies have been able to simultaneously address both topics to provide an integrated understanding of how energy pathways leading to higher trophic levels vary over time and space.

Production in lakes comes from both autochthonus (benthic and pelagic) and allochthonus (terrestrial) sources (Forbes 1887; Lindeman 1942; Pace *et al.* 2004), which can vary in importance depending on environmental conditions. For instance,

shallow lakes can be clear or turbid, leading to differences in the relative distributions of littoral, pelagic, and demersal habitats (Scheffer *et al.* 1993); while in other lakes, the amount of terrestrial carbon inputs can modify the relative importance of allochthonous and autochthonous carbon sources (Weidel *et al.* 2008; Solomon *et al.* 2011). In both examples, environmental conditions drive the distribution of available resources and can modify energy pathways supporting higher trophic levels, including fish. In most studies, energy pathways are evaluated at the individual level but combined to describe the population level niche. This assumes that consumers are mobile and able to integrate resources across a variety of habitats (Vander Zanden *et al.* 2002; Weidel *et al.* 2008) and resource use only differs slightly across individuals. However, many species exhibit individual specialization, with individuals foraging on only a subset of all resources used by the population (Bolnick *et al.* 2003), which reduces food web connectivity (Quevedo *et al.* 2009). Food web models that fail to incorporate this specialization may misrepresent a population's resource use and niche breadth, and how this changes in response to ecosystem perturbations.

Individual specialization occurs when individual niche breadth only overlaps with a subset of the population niche breadth. Growing empirical evidence suggests such specialization is common, with recent research focusing on what drives the degree of individual specialization within a population (Bolnick *et al.* 2003; Svanbäck and Persson 2009). Density has emerged as a key driver for presence/absence of trophic polymorphism in populations, an extreme example of individual specialization. At low densities, intraspecific competition is weak, limiting specialization and development of different morphs. At high densities, intraspecific competition is

strong increasing specialization and leading to disruptive selection for different morphs (Svanbäck and Persson 2009). Furthermore, at high densities, some individuals may switch from preferred to secondary prey, increasing individual specialization while expanding the total population niche (Araújo *et al.* 2008). Since population density can influence individual and population niche breadth, it can be expected that energy pathways supporting production at higher trophic levels will also change at different densities. Further development in this area has been limited by a lack of datasets that possess both the resolution and length to determine the degree of specialization within a population and the abundance of different specialists under a variety of environmental conditions and population densities.

Here, I evaluated population density and ecosystem state as drivers of resource and habitat use by individual specialists in a generalist population. I integrated data on littoral and demersal age-0 yellow perch diets and stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) with catch statistics to determine benthic reliance of the total population. The extent of benthic reliance is compared across different population densities during eutrophic and mesotrophic lake trophic states. I hypothesize that: 1) ecosystem state and population density interact to define the degree of benthic energy use of age-0 yellow perch, and 2) by altering resource use to take advantage of fluxes in pelagic and benthic energy pathways during their first year of life, yellow perch will be resilient to changes in lake trophic state.

METHODS

Study site and species

Oneida Lake, New York is a large, shallow lake (area 207 km^2, maximum depth 16.6 m, mean depth 6.8 m) located in the fertile plain of Lake Ontario, and is the site of a long-term monitoring program conducted by the Cornell Biological Field Station (CBFS). During ice-free months, the lake is well mixed and isothermal, though brief periods of stratification and hypolimnetic anoxia occur in some years. During the 1960-1970s, the lake was eutrophic with total phosphorus (TP) levels greater than 100 mg L^{-1}. The lake is currently mesotrophic with TP ranging from 15-30 mg L^{-1} (Mayer *et al.* 2002; Zhu *et al.* 2006; Mayer *et al.* in press). The shift in trophic state was primarily driven by reductions in nutrient loading and the introduction of zebra mussels (*Dreissena polymorpha*) in 1991. Zebra mussel effects included increases in water clarity, elevated benthic primary production, and an expansion of the littoral zone (Zhu *et al.* 2006; Mayer *et al.* in press). The fish community of Oneida Lake is dominated by walleye (*Sander vitreus*) and yellow perch (*Perca flavescens*), though species composition has changed over time resulting in a diversification of both prey and predator communities (Irwin *et al.* in press).

Yellow perch are generalists that exhibit a complex ontogeny, occupying all habitats of Oneida Lake (Clady 1976; Irwin *et al.* 2009). Adult yellow perch spawn in mid-May in littoral habitats, laying egg strands onto macrophytes and other littoral structures. Following hatching, fry are transported via water currents to offshore habitats where they feed primarily on zooplankton for one to two months (Noble 1975; Mills and Forney 1981; Mills and Forney 1988). At approximately 1.0 gram (mid-

July), age-0 yellow perch transition from limnetic to littoral and demersal habitats, and continue to occupy these habitats throughout the summer and fall, consuming zooplankton and macroinvertebrates (Mayer *et al.* 2000). In Oneida Lake, little is known about the importance of littoral habitats to age-0 yellow perch production and population dynamics, as most previous research has focused on limnetic and demersal habitats (Irwin *et al.* 2009; but see Clady 1976).

Field collections and archived samples

Age-0 yellow perch population dynamics have been monitored in Oneida Lake for over 50 years. Sampling began each year in early June and continued throughout the growing season using a variety of gears across life stages and habitats (see Irwin *et al.* 2009 for more details). Since 1961, demersal yellow perch have been sampled with a bottom trawl (5.5 m footrope, 13 mm cod end) weekly from July through October at 10 standard sites (Figure 3.1) at depths of 6 m (4 sites), 8 meters (2 sites) and 12 meters (4 sites). Littoral age-0 yellow perch were sampled using a beach seine (23 m by 1.5 m; 6 mm mesh) at 9 standard sites (Figure 3.1) during a subset of the years when trawling was conducted (~20 years). Sampling locations were consistent across all years in both surveys. In all surveys, catch was identified to species, counted, and a subsample measured for total length. A subsample of the catch from each survey date was archived and either preserved in formaldehyde or frozen (Table 3.1). Formaldehyde preserved samples were fixed in 1:10 formaldehyde:water solution immediately after collection.

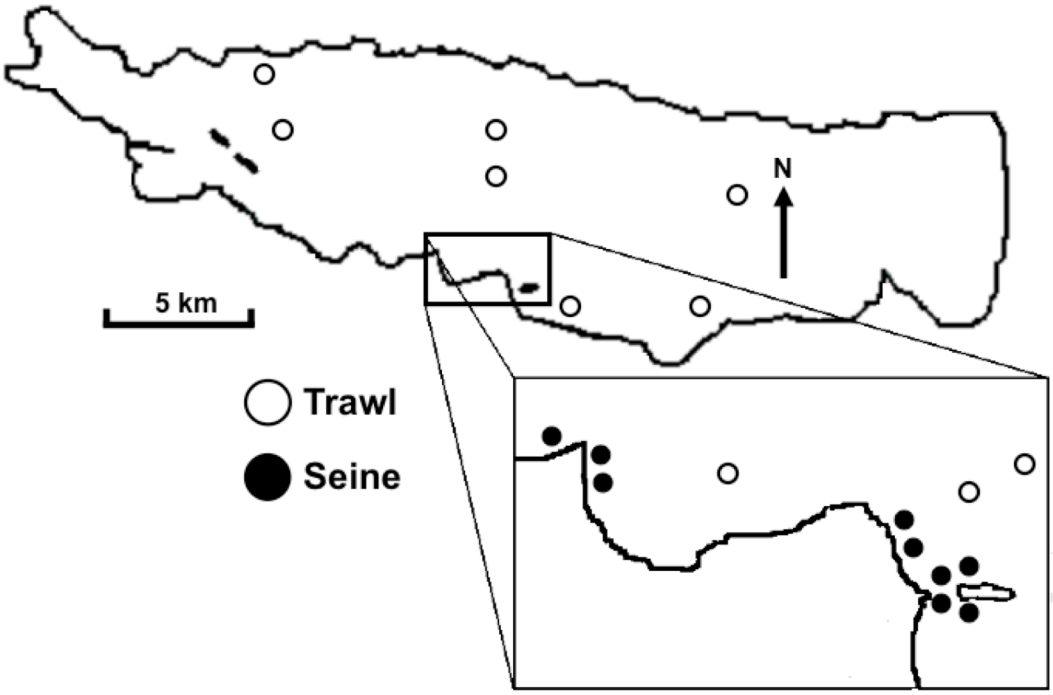

Figure 3.1. Map of Oneida Lake indicating long-term seine and trawl sampling locations.

Table 3.1. Summary table of samples and analyses by month/year. Month/year sampled, preservation technique, age-0 yellow perch density (18 mm, trawl, seine), C_{ws} from cluster analysis, age-0 yellow perch Bhattacharyya distance (B dist), individual percent benthic reliance for demersal and littoral age-0 yellow perch, and percent benthic reliance of age-0 yellow perch population at α_{bs} = 0.25, 0.43, and 0.7.

Year	Month	Preservation	18 mm (#/ha)	Trawl (#/ha)	Seine (#/ha)	C_{ws}	B dist	Demersal (%)	Littoral (%)	% Benthic (α=0.25)	% Benthic (α=0.43)	% Benthic (α=0.7)
1965	July	Formaldehyde	154110	36808	8252	**0.11**	1.35	0.22	81.31	5.86	11.95	28.07
1965	August	Formaldehyde	-	14948	1649	**0.34**	0.95	0.62	39.94	2.01	3.64	8.67
1966	July	Formaldehyde	44220	25188	4683	**0.29**	1.21	17.03	46.35	18.74	20.64	25.90
1966	August	Formaldehyde	-	4762	1632	**0.11**	1.96	2.37	42.93	6.53	10.70	20.39
1967	July	Formaldehyde	67320	36199	6003	**0.05**	0.48	7.06	2.72	6.83	6.58	5.85
1967	August	Formaldehyde	-	14107	4329	**0.15**	1.59	7.49	37.27	10.25	13.09	19.92
1970	July	Formaldehyde	88000	25489	14180	**0.15**	0.86	-2.77	43.77	4.51	10.99	23.52
1970	August	Formaldehyde	-	7848	4744	**0.27**	1.14	9.98	55.53	17.62	24.25	36.63
2007	July	Freeze	138760	13631	9769	**0.11**	1.45	13.37	66.79	23.67	32.12	46.80
2007	August	Freeze	-	6950	6840	**0.29**	2.91	18.11	93.83	36.81	50.37	70.86
2008	July	Freeze	67680	2038	20915	**0.21**	1.75	8.41	79.97	63.78	71.78	77.10
2008	August	Freeze	-	849	4518	**0.33**	2.33	7.92	78.94	53.35	64.78	73.65
2009	July	Freeze	125621	5338	8837	0.00	2.33	4.21	76.95	30.08	44.60	61.99
2009	August	Freeze	-	3184	6374	**0.18**	1.92	-2.6	78.23	29.75	46.03	63.98
2011	July	Freeze	4713	330	2785	**0.14**	2.75	7.07	76.92	58.59	67.43	73.54
2011	August	Freeze	-	130	1110	**0.18**	5.54	7.49	78.22	59.80	68.70	74.83

Stomach contents and stable isotope analysis

Diet composition and stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) of age-0 yellow perch were analyzed to provide short- and long-term indicators of niche breadth and individual specialization on pelagic and benthic energy pathways. Reliance on terrestrial carbon was not accounted for and assumed to be low due to Oneida Lake's large size and trophic state. Analyses were conducted on samples from eight years that represented two distinct ecosystem states (Mayer *et al.* in press): pre-dreissenid introduction (eutrophic; 1965, 1966, 1967, 1970) and post-dreissenid introduction (mesotrophic; 2007, 2008, 2009, 2011; Table 3.1). Within each time period, two high density years (1965, 1970, 2007, 2009) and two low density years (1966, 1967, 2008, 2011) were analyzed (Table 3.1). Classification of high and low density years was based on the density estimates of age-0 yellow perch during their limnetic stage at 18 mm (Rudstam and Jackson 2012). Within each year, analyses focused on age-0 yellow perch collected during July and August to evaluate individual specialization and energy pathway use during and after the transition from limnetic to littoral and demersal habitats. Within each month, 20 fish from each habitat were analyzed.

Diet composition was used to determine short-term foraging behavior and evaluate the potential for individual specialization by yellow perch in demersal and littoral habitats. Stomach contents were defined as diet items from the esophagus to the pylorus and enumerated based on broad taxonomic groups; including cladocerans, copepods, amphipods, chironomids, isopods, Trichopterans, and other macroinvertebrates. To evaluate if resource use by littoral and demersal yellow perch showed divergence, the presence/absence of demersal and littoral foraging clusters

was determined using complex network analysis (Araújo *et al.* 2008). In short, an "individual niche overlap network" was constructed, where nodes represent individuals and edges measure diet overlap among pairs of individuals. The weighted clustering coefficient C_{ws} was used to quantify degree of clustering, comparing overall density of connections in the network to the density of connections around individual nodes. C_{ws} varies from -1 to 1, where -1 represents continuous diet variation, zero represents a total random network, and 1 represents clustering on subsets of resources. The null hypothesis that $C_{ws} = 0$ was tested using a bootstrap procedure. DIETA was used to conduct all calculations, and Pajek (Batagelj and Mrvar 1998) was used to draw networks, visualize clusters, and assign individuals to *w*-cliques (see Araújo *et al.* 2008 for a detailed explanation).

Stable isotopes were used to complement diet analyses by providing an integrated picture of long-term foraging patterns to determine: 1) temporal extent of specialization, and 2) potential movement patterns between habitats. Stable isotope ratios of carbon and nitrogen ($\delta^{13}C$ and $\delta^{15}N$) were used to differentiate between benthic and pelagic energy pathways and establish trophic positions of individual age-0 yellow perch. Primary consumers collected during the diet analyses were used to provide time-integrated values of carbon and nitrogen sources at the base of the food web (Vander Zanden and Rasmussen 1999). Dorsal muscle was dissected from 20 littoral and 20 demersal age-0 yellow perch (40 total) used in the diet composition analyses. Lipid extraction performed on 10 fish indicated no significant effect of lipids on $\delta^{13}C$ or $\delta^{15}N$ ratios; therefore, lipids were not removed from samples used in the analyses. Invertebrate and fish tissue samples were dried for at least 48 h at 60ºC.

Dried samples (1 ± 0.1 mg) were packed into tin capsules for $\delta^{13}C$ and $\delta^{15}N$ analyses. Analyses were performed using a Thermo Delta V isotope ratio mass spectrometer interfaced to a NC2500 elemental analyzer at the Cornell Isotope Laboratory (Ithaca, New York, USA). Stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) were expressed as parts per thousand deviations from a chemical methionine standard. A subsample was analyzed in duplicate, and the analytical error was 0.27‰ for $\delta^{13}C$ and 0.12‰ for $\delta^{15}N$. Trophic position and proportion of benthic reliance of each individual were estimated from the isotopic ratios of muscle tissue, using a two end-member mixing model (Post 2002). Benthic and pelagic end members were assigned as the average isotopic signature of yellow perch diet items collected in littoral and demersal habitats, respectively. The Bhattacharyya distance, which measures similarity of multivariate distributions, was calculated to determine divergence of littoral and demersal diet items and age-0 yellow perch populations using the raw $\delta^{13}C$ and $\delta^{15}N$ stable isotope ratios for each year and month.

Population and carbon source estimation

Catch statistics and stable isotope samples were integrated to provide an estimate of the benthic reliance of the entire age-0 yellow perch population. Catch-per-unit-effort (CPUE) in demersal and littoral habitats was determined from trawl and seine surveys, and converted to density using the average area sampled by each gear. For each year, linear regression was used to fit catch-curves to the decline in the natural logarithm of density over time, assuming a constant mortality rate (Rudstam and Jackson 2012). Catch-curves were used to estimate abundance on July 15 and

August 15, which corresponded to sampling dates used for stable isotope analysis. In some years, problematic data points were excluded if their residuals from first fit regressions exceeded three times the interquartile range. Percent benthic support of the population was determined using the following equation:

$$\%Benthic_{Pop} = \frac{\alpha_{bs} \times \%Benthic_{bs} \times Density_{bs} + (1-\alpha_{bs}) \times \%Benthic_{tr} \times Density_{tr}}{\alpha_{bs} \times Density_{bs} + (1-\alpha_{bs}) \times Density_{tr}}$$

Where α_{bs} represents the estimated proportion of the lake that represents littoral habitats, *% Benthic*$_x$ represents the average benthic reliance of age-0 yellow perch captured in the trawl (*tr*) or seine (*bs*), and *Density*$_x$ represents the habitat-specific density. α_{bs} was set at 0.25, 0.43, and 0.7 based on observed and predicted changes in the area of littoral habitats before and after dreissenid mussel establishment (Fitzgerald *et al.* in press).

Statistical analyses and model selection

Analysis-of-variance (ANOVA) was used to test for significant effects of predictors (*i.e.,* habitat, time period, density, and their interactions) across all response variables. Within a year, July and August were treated as independent observations to increase sample size. Habitat, time period, density, and their interactions were used as predictors for analyses of individual percent benthic reliance and specific diet items (e.g. amphipods, cladocerans, copepods, chironomids, and Trichopterans; Table 3.2). Time period, density and their interactions were used as predictors for C_{ws}, baseline Bhattacharyya distance, age-0 yellow perch Bhattacharyya distance, and benthic

Table 3.2. ANOVA model selection and coefficients summary table for diet and individual benthic reliance analyses. Candidate models testing relationships between number per diet or individual age-0 yellow perch percent benthic reliance and habitat (Littoral), time period (Eutrophic), density (Low), and their interactions. AICc, Akaike weights (w_i), and evidence ratios (w_1/w_i) are included for those candidate models with evidence ratios < 10. Significant model coefficients are indicated in bold. Constants correspond to demersal habitats at high densities during mesotrophic conditions; therefore, coefficients correspond to littoral habitats, eutrophic conditions, and low densities.

Candidate Model	Intercept	Littoral	Eutrophic	Low	Eutrophic: Low	Eutrophic: Littoral	Littoral:Low	Eutrophic: Littoral: Low	Δ AIC$_c$	w_i	w_1/w_i
Amphipods											
Habitat x Time Period + Density	**1.34**	**3.76**	-0.58	**-0.79**		**-1.68**			-	0.41	-
Habitat x Time Period x Density	**1.60**	**2.91**	-0.99	-1.36	0.85	-0.23	1.73	-2.91	1.90	0.16	2.59
Habitat x Time Period	**0.96**	**3.74**	-0.60			**-1.66**			2.01	0.15	2.73
Habitat + Time Period + Density	**1.72**	**2.98**	**-1.43**	**-0.79**					2.45	0.12	3.41
Time Period x Density + Habitat	**1.58**	**2.97**	**-1.11**	-0.48	-0.65				3.81	0.06	6.71
Habitat x Density + Time Period	**1.80**	**2.82**	**-1.43**	**-0.95**			0.33		4.30	0.05	8.60
Habitat + Time Period	**1.35**	**2.96**	**-1.44**						4.36	0.05	8.85
Cladocerans											
Habitat x Time Period x Density	**166.14**	**-161.32**	**-137.76**	**135.08**	**134.90**	**149.27**	**132.49**	**-129.49**	-	1.00	-
Copepods											
Habitat x Time Period	**34.25**	**-28.79**	**-25.02**			**19.81**			-	0.50	-
Habitat x Time Period + Density	**33.06**	**-28.86**	**-25.07**	2.51		**19.59**			1.34	0.26	1.96
Habitat x Time Period x Density	**313.09**	**-21.87**	**-27.56**	6.67	4.82	**18.43**	-14.14	2.98	1.70	0.22	2.34
Chironomids											
Time Period x Density + Habitat	0.39	0.74	0.04	**2.08**	**-2.68**				-	0.48	-
TIme Period x Density	0.75		0.06	**2.10**	**-2.69**				0.47	0.38	1.26
Trichoptera											
Habitat x Time Period	0.02	**0.62**	-0.02			**-0.60**			-	0.66	-
Habitat x Time Period + Density	-0.01	**0.62**	-0.02	0.05		**-0.60**			1.79	0.27	2.45
Percent Benthic Reliance											
Habitat x Time Period x Density	**9.37**	**70.42**	-7.18	-0.03	6.59	**-17.47**	-0.40	**-27.79**	-	1	-

reliance of the age-0 yellow perch population (at a_{bs} = 0.25, 0.43, 0.7; Table 3.3). In all analyses, the best fitting, most parsimonious model of all candidate models was selected using Akaike's Information Criterion (AIC; Burnham and Anderson 1998). All analyses were conducted using the statistical software R (R Core Team 2012).

RESULTS

Diet analyses

Diet composition of age-0 yellow perch consistently indicated habitat-specific foraging patterns during both time periods. Zooplankton were the most common diet items in demersal-caught age-0 yellow perch. In contrast, benthic invertebrates were the most common diet items in age-0 yellow perch captured in littoral habitats. For all diet items, AIC identified habitat and time period as the most important predictors of diet, though density was also important for some prey (Table 3.2). All top models included interaction terms, with habitat – time period interactions occurring most frequently; a result of stronger foraging divergence between habitats during the 2000s. Resource clustering (C_{ws}) was significantly different from zero in all months and years, except July 2009 (Table 3.1), and demonstrated clear specialization both within and across littoral and demersal habitats (Figure 3.2). Results from individual diet items and cluster analysis are consistent with habitat-specific foraging specialization, but there was little evidence that time period, density, or time period x density interactions influenced clustering (Table 3.3).

Table 3.3. ANOVA model selection and coefficients summary table for clustering, stable isotope, and benthic reliance analyses. Candidate models testing relationships between C_{ws} (clustering), baseline Bhattacharyya distance, age-0 yellow perch Bhattacharyya distance, or benthic production (at a = 0.25, 0.43, 0.7) with time period (Eutrophic), density (Low), and their interactions. AICc, Akaike weights (w_i), and evidence ratios (w_1/w_i) are included for those candidate models with evidence ratios < 10 are included. Significant model coefficients are indicated in bold. Constants correspond to high densities during mesotrophic conditions; therefore, coefficients correspond to eutrophic conditions and low densities.

Candidate Model	Intercept	Eutrophic	Low	Eutrophic: Low	Δ AIC$_c$	w_i	w_1/w_i
C_{ws}							
Time Period + Density	**0.18**	0.004	0.001		-	0.39	1.00
Time Period x Density	**0.15**	0.07	0.07	-0.14	1.25	0.21	1.87
Density	**0.18**		0.001		1.36	0.20	1.97
Time Period	**0.18**	0.004			1.36	0.20	1.98
Baseline Bhattacharyya Distance							
Time Period	**2.62**	**-1.52**			-	0.62	1.00
Time Period + Density	**2.30**	**-1.52**	0.64		1.19	0.34	1.81
Bhattacharyya Distance							
Time Period	**2.62**	**-1.43**			-	0.53	1.00
Time Period + Density	**2.33**	**-1.43**	0.59		0.82	0.35	1.51
Time Period x Density	**2.15**	-1.08	0.94	-0.71	3.19	0.11	4.93
Benthic Production (α = 0.25)							
Time Period x Density	**30.08**	**-22.58**	**28.80**	**-25.72**	-	1.00	1.00
Benthic Production (α = 0.43)							
Time Period x Density	**43.28**	**-30.57**	**24.89**	**-24.85**	-	0.99	1.00
Benthic Production (α = 0.7)							
Time Period x Density	**60.91**	**-36.69**	**13.87**	**-20.08**	-	0.50	1.00
Time Period	**67.84**	**-46.73**			0.64	0.36	1.38
Time Period + Density	**65.93**	**-46.73**	3.83		2.60	0.14	3.66

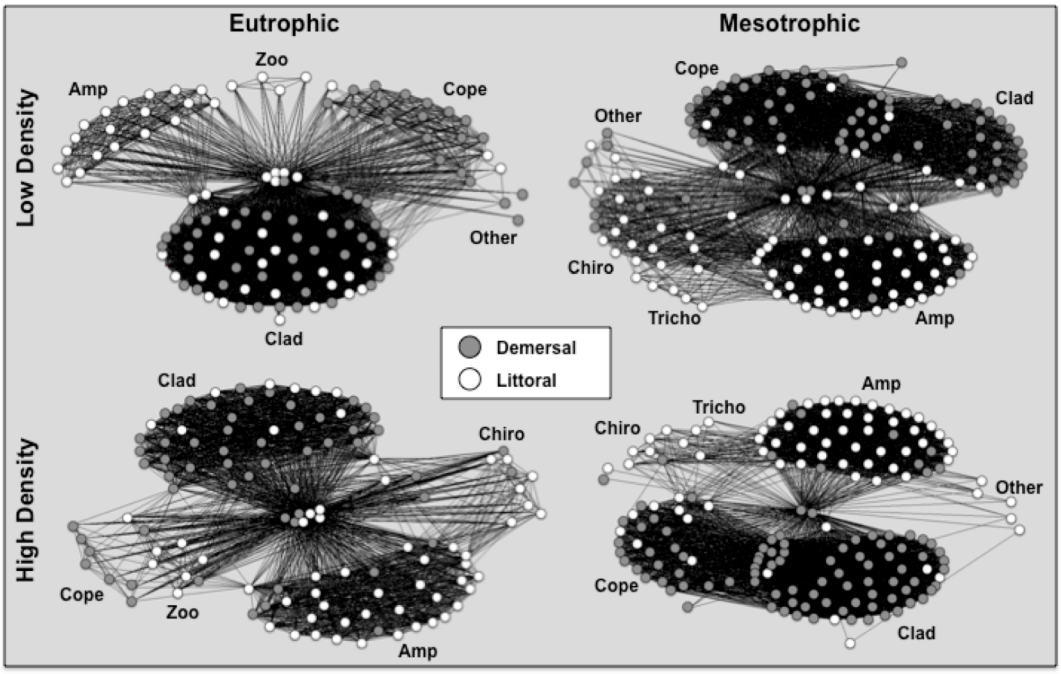

Figure 3.2. Age-0 yellow perch foraging clusters. Age-0 yellow perch foraging clusters in demersal and littoral habitats during eutrophic and mesotrophic conditions at high and low densities. Clusters are labeled according to major diet items and include amphipods (Amp), chironomids (Chiro), cladocerans (Clad), copepods (Cope), Trichopterans (Tricho), zooplankton (Zoo) and other (Other) diet items.

Stable isotope analysis

Bachattacharyya distance indicated a strong divergence in the $\delta^{13}C$ and $\delta^{15}N$ of diet items from age-0 yellow perch collected in demersal and littoral habitats (Figure 3.3). Pelagic and benthic signatures differed as expected for a north temperate lake (Figure 3.3). Divergence increased during the 2000s, but there were no differences between high and low density years (Table 3.3). $\delta^{13}C$ and $\delta^{15}N$ of age-0 yellow perch exhibited a similar littoral-demersal divergence that was clearly visible during 15 out of 16 month/year combinations (Figure 3.4). Bhattacharyya distance of age-0 yellow perch $\delta^{13}C$ and $\delta^{15}N$ increased during the 2000s, and there was some evidence that divergence increased at high densities (Table 3.3). In all years, resource use by demersal fish clustered around 0% benthic reliance, while littoral fish exhibited more complicated patterns. These ranged from almost 100% benthic reliance to a continuum across the pelagic-benthic spectrum (Figure 3.4). Benthic reliance varied across habitats, time periods, densities, and interactions between time period and density. These differences were driven by changes in littoral habitats, as benthic reliance was consistently low in demersal habitats (Table 3.1). In littoral habitats, age-0 yellow perch percent benthic reliance increased in the 2000s, but density had a weaker effect than in the 1960s (Table 3.2).

Habitat-specific population densities

During the 1960s, age-0 yellow perch were consistently denser in demersal habitats at 1.5 to 9 times the density in littoral habitats. During the 2000s, this pattern switched as littoral densities ranged from approximately equal to 10 times the

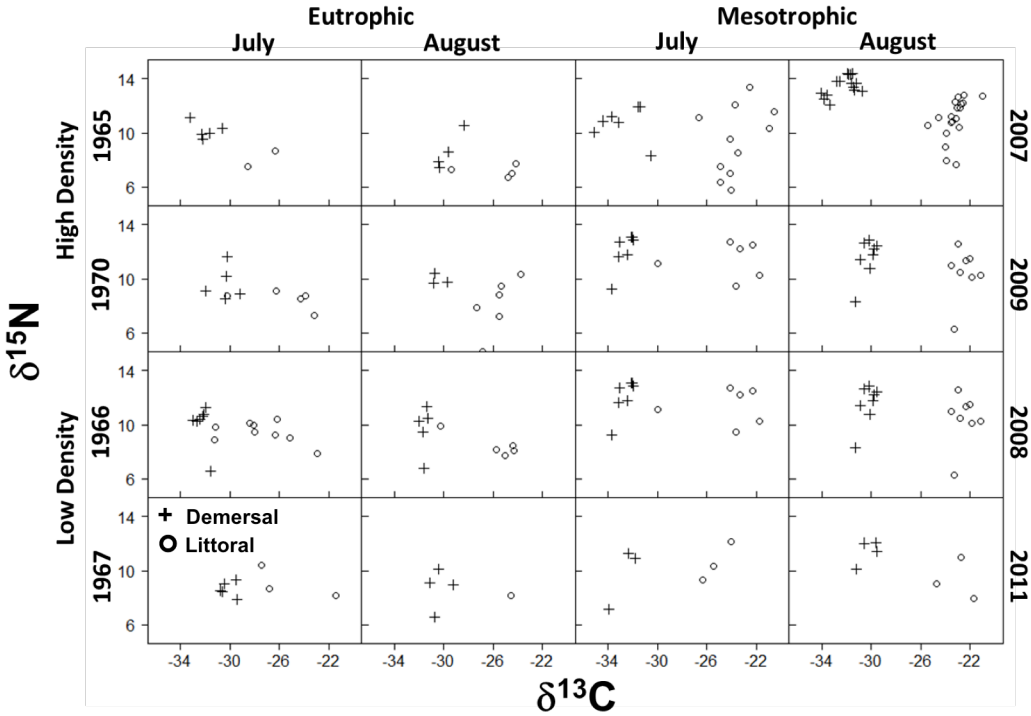

Figure 3.3. Dual isotope plots for age-0 yellow perch diet items. $\delta^{13}C$ and $\delta^{15}N$ ratios for diet items collected from fish sampled in littoral and demersal habitats presented by month and year.

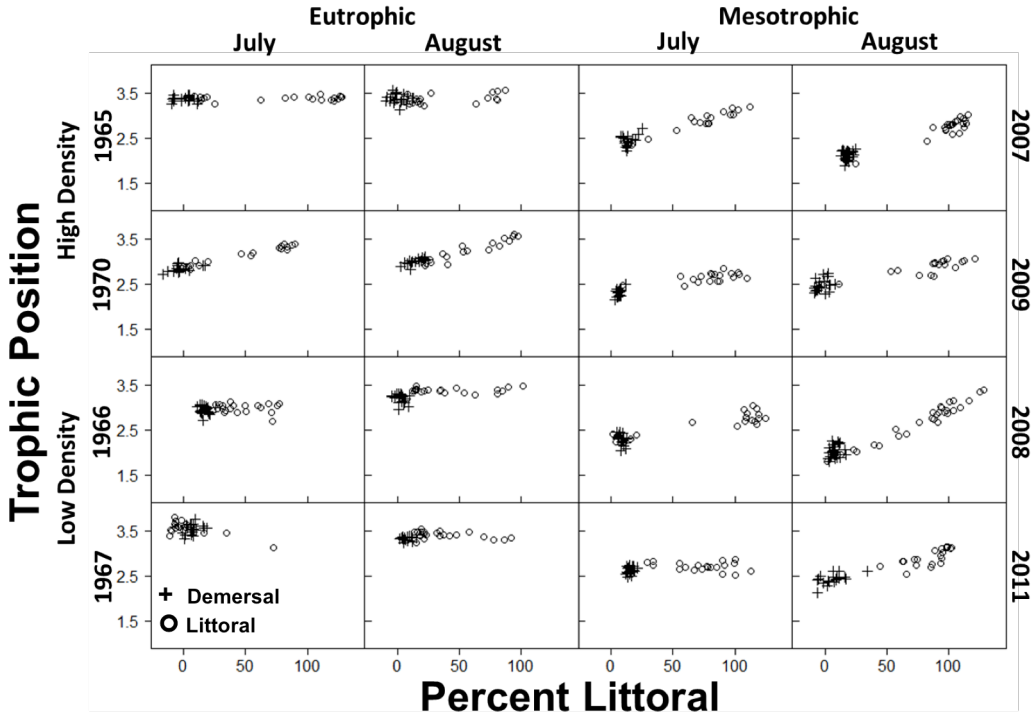

Figure 3.4. Percent littoral reliance and trophic position for age-0 yellow perch. Percent littoral reliance and trophic position of age-0 yellow perch collected from littoral and demersal habitats presented by month and year.

densities in demersal habitats (Table 3.1). Demersal densities fluctuated by almost three orders of magnitude (range 130-36,808 fish/ha) and declined on average from approximately 20,000 fish in the 1960s to 4,000 fish per hectare in the 2000s (Table 3.1). Littoral densities fluctuated by two orders of magnitude (range 1,110-20,915 fish/ha) and in all but two month/year combinations range from 1,000 to 10,000 fish per hectare. Littoral density showed little change between the 1960s and 2000s, at 5,684 and 7,644 fish per hectare, respectively (Table 3.1).

Population-level benthic reliance

Integration of stable isotope signatures and habitat-specific catch statistics indicated that time period, density and time period x density interactions drove energy pathways supporting age-0 yellow perch production (Table 3.3). During the 2000s, age-0 yellow perch benthic reliance was highest, and the strength of the density effect increased as densities became higher in littoral relative to demersal habitats (Table 3.1, 3.3). These results were consistent regardless of whether the proportion of the lake defined as littoral habitat (a_{bs}) was set at 0.25, 0.43, or 0.7; though the likelihood of the density effect decreases at $a_{bs} = 0.7$ (Table 3.3).

DISCUSSION

Intraspecific specialization, ecosystem state, and density

Bhattacharyya distance indicated that time period had the greatest effect on the degree of divergence between littoral and demersal habitats while density had less of an effect. Reductions in nutrient loading and the introduction of dreissenid mussels

between time periods resulted in wide-scale ecological changes characterized by increases in water clarity, shifts from pelagic to benthic production, and an expansion of the littoral zone ("benthification"; Zhu *et al.* 2006; Higgins and Vander Zanden 2010; Fitzgerald *et al.* in press). As water clarity increased, pelagic and benthic energy pathways leading to age-0 yellow perch appear to have become more distinct in littoral and demersal habitats at the level of primary consumers (Table 3.2; Figure 3.3). Littoral prey items became more enriched in $\delta^{13}C$ and patterns of divergence (baseline Bhattacharyya distance) in diet items match those observed in age-0 yellow perch. This indicates increased separation of benthic and pelagic energy pathways that may be strengthened by fish behavior and habitat selection. For example, during eutrophic conditions, $\delta^{13}C$ ratios of littoral age-0 yellow perch consistently spanned across the entire carbon continuum due to less specialization on either benthic invertebrates or zooplankton, or consistent movement from demersal to littoral habitats. In contrast, following dreissenid introductions, consumption of zooplankton by littoral age-0 yellow perch decreased while consumption of benthic invertebrates increased, and littoral age-0 yellow perch $\delta^{13}C$ values became more clustered in most years, but not all.

Theory predicts that individual specialization should increase at higher population densities through either exploitative or interference competition (Svanbäck and Persson 2009). At high densities, intraspecific competition for limited resources is stronger and requires that individuals specialize on a subset of the total niche (*i.e.,* exploitative). Similarly, a subset of individuals may occupy optimal habitats, displacing other individuals to suboptimal habitats where resources are not as good

(*i.e.,* interference; Post *et al.* 1997). At low densities, specialization is unnecessary due to low intraspecific competition for abundant resources (Svanbäck and Persson 2009), or a lack of saturation in optimal habitats (Post *et al.* 1997). In my data set, individual specialization occurs in all years, regardless of population density, and there is not a strong relationship between population density and my metrics of littoral-demersal divergence.

I suspect the lack of relationship between density and littoral-demersal divergence is driven by the fact that these metrics do not take into consideration how population density influences the distribution of specialists within the population. In species where specialization occurs in all years, understanding population density effects on specialization requires an understanding of how specialists are distributed within the population. Age-0 yellow perch exhibited individual specialization in all years of this study regardless of time period (Figure 3.4). The effect of density on divergence between these two habitats was minimal compared to its effect on the distribution of age-0 yellow perch across habitats. At low densities, a larger proportion of individuals within the population were littoral specialists, elevating the importance of benthic energy pathways (Table 3.1). At high densities, individuals within the population were primarily demersal specialists, elevating the importance of pelagic energy pathways (Table 3.1). By incorporating density, the patterns observed for age-0 yellow perch follow theoretical predictions about interactions between individual specialization and density (Svanbäck and Persson 2009). These results suggest that littoral specialization is likely the most optimal foraging strategy, but

pelagic specialization occurs at high densities due to stronger intraspecific competition.

Use of multiple energy pathways

Variation in the distribution and degree of specialization across habitats changes how species interact with their environment, ultimately driving which energy pathways support production at higher trophic levels. Benthic reliance of age-0 yellow perch illustrates this point and demonstrates that energy pathways supporting production of consumers can vary on both short- and long-term time scales (Carpenter and Turner 2000). Over the long-term, ecosystem state dictates the magnitude of different energy pathways available to consumers (*i.e.,* lake trophic status and the presence/absence of dreissenid mussels). At shorter time scales, patterns of habitat use change based on abundance, altering the relative importance of different energy pathways to consumers.

In Oneida Lake, there was less differentiation between littoral and demersal habitats when the lake was eutrophic and pelagic energy pathways primarily drove production of age-0 yellow perch. During mesotrophic conditions, benthic energy pathways in littoral habitats increasingly drove age-0 yellow perch production (Table 3.1; Figure 3.4). In both time periods, inter-annual variability of carbon use was driven by population density, which influenced habitat use and distribution of benthic and pelagic specialist within the population. At high densities, a greater proportion of the population used demersal habitats, and benthic reliance of the whole population decreases. Conversely, at low densities, age-0 yellow perch primarily used littoral

habitats, resulting in greater reliance of the population on benthic energy pathways. I propose that ecosystem state defines the range of benthic support of fish populations, while population density determines where along the potential range a fish population will occur within a specific year.

In my analyses, I explored effects of ecosystem state and density under three scenarios of habitat distributions (a_{bs} = 0.25, 0.43, and 0.7; Fitzgerald *et al.* in press), and assumed that distributions did not change over time. This assumption leads to conservative estimates of the effect of environmental conditions on the importance of different energy pathways to age-0 yellow perch production. In Oneida Lake, increases in water clarity led to an expansion of the littoral zone from 25% to 43% of lake surface area as the photic zone expanded to include more benthic surface area (Fitzgerald *et al.* in press). Under this assumption, age-0 yellow perch benthic reliance increased from approximately 2-20% to 30-70%, with lower reliance associated with higher densities. Failure to incorporate information on density and resource use from both demersal and littoral habitats would have led me to inaccurately conclude that age-0 yellow perch benthic energy reliance did not shift with changing ecological conditions.

These results represent a step forward towards understanding short- and long-term drivers of energy pathways supporting consumer production (Weidel *et al.* 2008), and shed light on underlying mechanisms of inconsistent and mixed responses of higher trophic levels (*i.e.,* fish) to introductions of dreissenid mussels (Higgins and Vander Zanden 2010). Much previous research on these topics has assumed fish are mobile, utilize multiple habitats, and integrate both benthic and pelagic production

(Vander Zanden and Vadeboncoeur 2002); therefore, population- and lake-wide changes can be evaluated by monitoring a single habitat. Though this may be true for some species, there is growing evidence that in many species and systems, individuals specialize on only a subset of available resources (Bolnick *et al.* 2003). Individuals within these populations may show inconsistent or even contradictory responses to ecological perturbations, making it difficult to make accurate conclusions about population level responses to perturbations.

Niche diversity and resilience

Across species and systems, the ability of a population to adapt to changes in habitat and resource distributions is likely context-dependent (Agrawal *et al.* 2007), and may explain inconsistencies of species responses to ecosystem changes across diverse systems (Higgins and Vander Zanden 2010). Further appreciation of the ability of individuals and populations to adapt to changing ecological conditions and a multiple habitat approach to studying ecological dynamics are needed to address these inconsistencies and aid our understanding of ecological responses to perturbations. Populations able to utilize multiple habitats and energy pathways (*e.g.,* benthic and pelagic) are likely to be more resilient to ecosystem perturbations. Habitat and resource specialists are more likely to be either positively or negatively impacted depending on the specific habitat they occupy. For instance, in Oneida Lake, yellow perch density in demersal habitats has decreased across all age-0 life stages; however, age-1 abundance has stayed constant or even increased (Irwin *et al.* 2009). I suspect

the stronger recruitment from littoral habitats, illustrated here, is an important factor driving the stability observed at age-1 (Fitzgerald *et al.* 2006).

The physical characteristics of a specific ecosystem should also influence the resiliency of a population to ecosystem perturbations. For instance, populations that occur in very shallow or deep lakes are unlikely to show as much resilience to ecosystem changes that cause declines in one habitat type because habitats will tend to be homogenous in lakes with these types of bathymetry. However, intermediate lakes that are not dominated by one habitat are likely to increase resilience of generalist populations because reduced profitability of one habitat can be compensated by increased profitability of another habitat, as was observed in Oneida Lake. Therefore, a higher diversity of resource use by a population should lead to greater resiliency to ecosystem changes. Conservation objectives should be established to maintain the diversity of individual specialist and resource use strategies within populations to allow adaptation to changing ecological conditions.

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CHAPTER 4

"MANAGER'S MODELS": A TOOL FOR GRADUATE STUDENTS TO LEARN HOW SCIENCE INFORMS MANAGEMENT

ABSTRACT

The complexity of fisheries management within the context of coupled socio-ecological systems requires an understanding of feedbacks between ecological and socio-economic components of the management system. Identifying these feedbacks is often difficult for fisheries students, scientists, and managers, limiting their ability to understand where science might best inform management. I propose the development of Manager's Models as a valuable tool to teach fisheries students: 1) the structure of the management system, 2) feedbacks between management actions and socio-ecological systems, and 3) where science informs management. I discuss my experiences conceptualizing a Manager's Model for Oneida Lake, New York, USA, to highlight feedbacks between major ecological and social components within this socio-ecological system. This approach provides students with an appreciation and familiarity with social aspects of fisheries management, by building on strong foundations in traditional fisheries curriculum, not detracting from them. Additionally, this experience develops professional and interpersonal skills necessary to contribute to management teams and prepares students for the challenges of decision making associated with management of complex socio-ecological systems. Fisheries scientists and managers can also benefit from this exercise, because it

provides a framework to incorporate both ecological and social knowledge into fisheries management.

INTRODUCTION

It is a common misconception among environmental scientists that once a researcher has published their findings, managers and policy makers will have access to the information and will use it to identify and achieve management and conservation objectives (Nadkarni and Stasch 2013). To address this disconnect, scientists are beginning to show greater interest and accept more accountability in conducting research that directly informs management and policy of environmental issues (Schlesinger 2010). The effectiveness of many scientists to achieve this goal is often limited by their scientific training, which typically focuses on developing expertise in natural not social sciences (Nadkarni and Stasch 2013). Fisheries research is directly tied to management and policy affecting aquatic and marine ecosystems and a strong legacy of successful collaborations exists among scientists, managers, and policy makers across many systems and species. As the complexity and scale of the challenges to sound fisheries management continue to increase, fisheries scientists need to possess a clear understanding of the broader socio-ecological networks that ecosystems are embedded within (Angermeier 2007).

Over the last 25 years, there has been a push to develop fisheries curricula that move beyond traditional training in ecological principles and fisheries techniques to include greater awareness of the socio-ecological systems fisheries are embedded within (Knuth 1987; Adelman *et al.* 1994). A major challenge emerging from this

discussion is how to provide students with a strong foundation in core fisheries biological and ecological concepts while incorporating additional coursework, such as human dimensions and integrated resource management (Gabelhouse 2010). Adelman *et al.* (1994) suggests not to make major changes to what is taught, but rather change how we teach through innovative teaching techniques, discussion groups, case studies, cooperative learning, practicums, capstone courses, and writing across the curriculum. Learning that occurs from these types of teaching techniques addresses the characteristics and educational needs of future fisheries professionals (*i.e.* the Millennials; Millenbah *et al.* 2011).

Several innovative teaching techniques have recently emerged including constructivist learning, where feedbacks between instructors and students direct the curriculum (Habron 2005), and hands-on experiences provide exposure to research and management topics (Myrick *et al.* 2013). These types of learning environments build student excitement and lead to higher retention of students in environmental sciences (Locks and Gregerman 2008; Myrick *et al.* 2013). In addition, students develop practical experiences working with fisheries scientists and managers. This immersion helps develop essential professional skills necessary to bridge the science-management gap, such as planning, consensus-building, and communication (Kroll 2007), develops the interpersonal skills necessary to contribute to management teams (Krasny *et al.* 2009), and prepares students for the challenges of decision making associated with management of complex socio-ecological systems (Krasny *et al.* 2009). Given the value of real-world learning experiences to student development and education, additional teaching techniques are needed that encourage identification of

direct and indirect feedbacks, increase awareness of alternative perspectives, and encourage creativity in problem solving.

I propose the development of Manager's Models as an interactive training exercise for graduate students to apply strong foundations in natural sciences (*e.g.,* ecology, limnology, fish biology) while gaining familiarity with the management process and appreciation for information needs that can be met by social sciences (*e.g.,* human dimensions, organizational theory, integrated resource management). Through this process, students can begin to conceptualize how their research informs management and conservation within the coupled socio-ecological system they work in and develop the interpersonal skills necessary to ensure the application of their research towards accomplishing management and conservation objectives. The goal of this analytical exercise is to build on a student's current knowledge base and not replace core biological and ecological curriculum, so individuals can be more effective team members and communicators throughout the management process. I begin with a brief introduction to Manager's Models and discuss their utility in combining ecological and human dimensions knowledge to conceptualize a coupled socio-ecological management system. These concepts are applied to Oneida Lake, NY following guidelines outlined by Decker *et al.* (2012) to illustrate the process of developing a Manager's Model and identify key components of the Oneida Lake socio-ecological system (OLS). As a summary, I discuss the value of this and similar exercises as learning tools that prepare students to address the complexity of current and future environmental challenges.

BUILDING A MANAGER'S MODEL

A Manager's Model is a conceptual framework for a management system that defines ecological and social components of the socio-ecological system, identifies linkages between components, and clarifies objectives and assumptions (Decker *et al.* 2012). Manager's Models complement adaptive resource management (Walters 1986), leading towards adaptive impact management (AIM) by integrating the biological understanding of the system with societal values through identification of fundamental and enabling objectives (Enck *et al.* 2006). Fundamental objectives indicate why management is needed and what should be accomplished through management actions to achieve a desired condition for the socio-ecological system (*i.e.* societal values). Enabling objectives specify outcomes, which aid in the identification of management actions needed to achieve fundamental objectives (*i.e.* overcoming ecological/societal constraints; Enck *et al.* 2006). By defining the organization structure and feedbacks within management systems, decision making can be improved through anticipation of unexpected outcomes and awareness of new opportunities to accomplish fundamental and enabling objectives (Decker *et al.* 2006).

At their core, Manager's Models are a soft-systems approach to situational analysis based on five key concepts necessary to integrate biological and societal knowledge into management decisions and actions (Decker *et al.* 2012):

Values: Human values are the core of fisheries management but often conflict based on psychological, social, economic, political, and cultural influences (Keeney 1992). Balancing and weighing conflicting values is an important component of management decisions.

Impacts: Impacts pertain to the effects that result from events or interactions with fisheries, stakeholders, and/or fisheries management interventions. Impacts can lead to both beneficial and negative effects, and managing the levels of these impacts is the primary focus of AIM (Decker *et al.* 2012).

Limits and Capacity: Limits and capacity applies to traditional ecological concepts (*e.g.,* carrying capacity), but also includes integration of social, economic, institutional, administrative, cultural, and legal limits and the capacity for society to tolerate change.

Scale: Scale represents the spatial, temporal and operational levels that must be considered to achieve management objectives, and requires an appreciation of ecological and societal boundaries of specific impacts.

Decision Making: Effective decision making is the primary responsibility of fisheries management, and includes, "the processes that (a) define the ends or fundamental objectives of management in terms of stakeholder-defined impacts and (b) develop socially acceptable interventions that result in desired changes in those impacts (Decker *et al.* 2012, pg. 8)."

Appreciation of these key concepts and their interactions is the basis for developing a Manager's Model, and should be considered at the outset and revisited throughout model development as more information is collected or societal values are revealed.

Development and conceptualization of the Manager's Model begins through communication between fisheries scientists, managers, and stakeholders to assess availability of knowledge that can be used to develop consensus on the key concepts discussed above. This information is used to articulate the conceptual model of the

management system (*i.e.,* Manager's Model), which identifies primary components of the system, their status or condition, and their connections, all of which should be revised as new information is acquired. A Manager's Model should be structured to clarify managers' perspectives about objectives and identify targets for management success that are expressed as ***desired future conditions***, which encompass broad, long-term goals for the entire socio-ecological system. Differences between desired future conditions and current conditions are met through both ***fundamental*** and ***enabling objectives*** that identify a range of desired outcomes and propose how these outcomes can be achieved, respectively.

Desired future conditions, fundamental objectives, and enabling objectives represent the backbone of most Manager's Models, but are supported by additional components that are likely to vary substantially across socio-ecological systems. These components can include indicators of socio-ecological conditions (*e.g.,* historical conditions, current conditions, management concerns, stakeholder concerns) or management actions and effects (*e.g.,* primary actions/interventions, collateral/subsequent impacts, mitigating actions). Interactions between components are linked based on the expected directionality of cause-effect relationships and the flow of information and outcomes.

Research and monitoring improve the sophistication of Manager's Models by reducing uncertainty and providing the information necessary to identify and develop linkages between different components. The availability of ecological and social knowledge differs substantially across socio-ecological systems, and it is important to ensure that both types of data are being considered when defining fundamental and

enabling objectives. This can help managers set ecological and social research priorities, and direct active-adaptive and passive-adaptive management interventions to aid in learning. Research and monitoring allows continued refinement of the Manager's Model as more data are collected through successive management cycles. This iterative process is critical to move from Impact Management (IM) to AIM, where the management performance is evaluated based on producing desirable outcomes, and the Manager's Model is consistently updated to provide a more accurate representation of reality.

To date, application of Manager's Models has been limited primarily to examples from wildlife management (Decker *et al.* 2006; Siemer 2009); however, there is no reason the framework for developing Manager's Models to implement AIM into fisheries would not be successful. Below, I discuss my experiences developing a Manager's Model for the OLS. The motivation for this project was to identify how/where my reseach informs management in the context of decision making within a socio-ecological system; however, I feel the process discussed within this paper is relevant to more than graduate-level training.

CASE STUDY: ONEIDA LAKE, NY

An inquiry-based approach was used to construct a Manager's Model for the OLS, in which I engaged in conversations with scientists, managers, and stakeholders within the Oneida Lake watershed. These conversations were often informal and unstructured providing an opportunity for individuals to express their opinions on perceived values, impacts, limits and capacity, scale, and decision-making. These

conversations were complemented with participation in formal meetings designed to facilitate communication between diverse interests within the watershed and to direct management decisions and interventions. The focus of these meetings ranged across spatial and operational scales. This inquiry-based approach differs from the more commonly applied facilitative approach (Decker *et al.* 2012), where managers and sometimes stakeholders are brought together and a discussion leader facilitates conceptualization of the Manager's Model. Both methods have their value; therefore, the method employed will likely vary based on available resources and the existing communication structure within the socio-ecological system.

Before constructing a Manager's Model, one needs to determine the appropriate scale to encompass the most important components and feedback loops within the socio-ecological system. For ease, I defined the watershed boundary as the primary system of interest, but acknowledge that ecological and social dynamics within these boundaries are often driven by outside influences. For instance, Oneida Lake is connected to the Great Lakes and New York Harbor via the Erie Barge Canal; therefore, food web dynamics within the lake are often driven by introductions of non-native species from outside of the watershed (*e.g.* dreissenid mussels). In discussing specific components of the OLS Manager's Model, my primary focus is limited to the Oneida Lake fishery. I feel this provides a logical bridge for discussing how fisheries sciences (both ecological and social) inform management of socio-ecological systems that is easily relatable to fisheries students, scientists, and managers.

DESCRIBING THE SOCIO-ECOLOGICAL SYSTEM

The first step in conceptualizing the Manager's Model was to describe the context and the ecological and social components of the socio-ecological system. This will differ across socio-ecological systems, and specific components chosen should by organized logically with clearly defined interactions. At this stage in development of the Manager's Model, participants should be encouraged to think broadly about the scale of the socio-ecological system to ensure that indirect or complex relationships are not excluded.

Desired Future Condition

The desired future condition represents a broad and generic goal for the specific management system of interest that encompasses a diversity of perspectives and includes both ecological and social aspects. Creating a broad vision of the desired goal for the system serves several purposes: 1) identifies feedbacks between ecological and social systems at the outset of model development, 2) provides a vision for the future of the socio-ecological system that is robust to changes in specific ecological or social conditions, and 3) unifies and promotes discussion from diverse interests across the watershed allowing further refinement of ideas about how to accomplish the desired goals as additional components are identified.

In the OLS, review of available management documents (CNY-RPDB 2004) coupled with discussions led me to describe the desired future condition as, "***Maintain Oneida Lake as a major ecological, economic, and sociological asset of the region.***"

Current Conditions

After a desired future condition was identified, I needed to evaluate it in light of current ecological and social conditions to highlight challenges to achieving or maintaining future goals. As fisheries scientists, an underlying motivation for many of our research questions is to describe ecosystem structure and function as it pertains to current conditions, but it is also important that we place this knowledge within the broader socio-ecological systems where we work. It is important to consider how humans influence the environment and how the environment influences humans. This can be achieved by focusing on feedbacks between social and ecological components and identifying cause and effect relationships beyond the water's edge.

A logical first step in defining current conditions is to synthesize available ecological and social knowledge bases and establish relationships between environmental and socio-economic indicators. Through this activity, students refine their skills synthesizing, analyzing, and articulating information from diverse sources to describe the current state of the socio-ecological system. Not surprisingly, most data available to assess the current state of the OLS focus on the environment and not the socio-economic system. The OLS has a wealth of environmental data available, likely more than most lake watersheds across North America. The legacy of environmental monitoring is strongly linked to a long-term partnership between Cornell University and the New York State Department of Environmental Conservation (NYS-DEC) focused on the work of the Cornell Biological Field Station (CBFS), which has monitored food web dynamics in the lake since the 1950s. Anglers on Oneida Lake primarily target walleye (*Sander vitreus*), yellow perch

(*Perca flavescens*), and smallmouth bass (*Micropterus dolomieu*). Some research has focused on feedbacks between the environment and humans, specifically impacts of anglers on the Oneida Lake fish community (Jackson *et al.* 2012) and the contributions of angling to the local economy (Connelly and Brown 2007; Shwiff *et al.* 2009). In the process of creating my OLS Managers' Model, it became clear that further elucidation of feedbacks within the OLS is needed, and will require acknowledgement of intentional/unintentional and direct/indirect interactions within the socio-economic components of the management system.

Historic Conditions

Historical conditions of socio-ecological systems provide both a baseline to evaluate current conditions and insight to make predictions about the directionality of future changes. This establishes the context to place the management system within the broader temporal scale, consider trajectories of various components, and can inform how observed and perceived differences between historic and current conditions determine both management and stakeholder concerns. In many management systems, substantial information on historical conditions is often lacking, requiring that scientists, managers, and stakeholders make assumptions about perceived relationships between ecological and social components. Building awareness of historical conditions is especially important for students because they are just beginning to become involved in the management system and need to establish context to appreciate interactions between social and ecological components within the Manager's Model.

As a result of the CFBS long-term monitoring program, much is known about the historical ecological conditions within Oneida Lake and its watershed since the 1950s. The fish community in the lake was primarily dominated by a relatively simple predator-prey dynamic between walleye and yellow perch (Forney 1980). As this fishery developed, local anglers established a strong attachment to these species, and relatively simple management criteria were identified to balance predator-prey dynamics in the lake and angler demand (Forney 1980). Interactions between scientists, managers, and stakeholders were relatively harmonious during this time period due to shared objectives and a low diversity of conflicting stakeholder interests. During the early 1980s, management increased in complexity as additional perspectives were incorporated into management objectives and management shifted beyond the lake boundaries to include a greater emphasis on the watershed. These changes began to shift management objectives from the ecological system towards the socio-ecological system; however, incorporation of socio-economic perspectives has progressed slowly and remains a challenge.

Research and Monitoring

Research and monitoring are critical components of the management cycle. Structure and function of ecological systems, societal values, and feedbacks between socio-ecological systems are all identified through research and monitoring, which provides the primary mechanism to develop new knowledge. This knowledge is used to verify assumptions and improve causal relationships between components of the socio-ecological systems, and evaluate the feasibility of alternative management

actions and interventions to achieve enabling objectives. Placing research and monitoring within the broader management system provides value to students by identifying where their research results will inform management and develops an appreciation for differences in how ecological and social knowledge are incorporated into the decision making process. Additionally, students become aware of key knowledge gaps within the management system, which can aid in the development of future research questions.

As noted above, lots of research and monitoring occurs within the OLS, though the emphasis is primarily focused on environment components. Research and monitoring within the lake is dominated by the CBFS, while data collection within the surrounding watershed is conducted by numerous entities, including local, state, and federal agencies, and research institutions (CNY-RPDB 2004). Research and monitoring of the socio-economic system are sparse and tend to be limited to descriptive analysis of demographic data available through the census (CNY-RPDB 2004). Some efforts have been made to develop more detailed analyses of causal relationships between environmental quality and the regional economy (Connelly and Brown 2007; Shwiff *et al.* 2009), but significant knowledge gaps exist and additional research would aid in the development of the OLS Managers' Model. This potentially limits managers from identifying and determining the feasibility of alternative interventions and limits their ability to anticipate collateral/subsequent impacts.

Management Concerns

Management concerns often focus on what should be done (*i.e.,* primary actions/interventions) to achieve desired ecological states (*i.e.,* enabling objectives) and are often a response to real or anticipated stakeholder concerns. These concerns vary within and across diverse management agencies and stakeholder groups, making it challenging to articulate clearly identifiable concerns that are ubiquitous across groups. In most cases, the diversity of concerns within the socio-ecological system is a major concern of managers but also an opportunity.

Identifying management concerns is a critical component of the Manager's Model, but is also an important component of student development. These experiences can increase communication between students, scientists, and managers, and can lead to connections with potential mentors within the scientific and management communities. By participating in the management process students develop an appreciation for the complexity of balancing social and ecological limitations when making decisions.

The OLS is no exception to this challenge given the diversity of management agencies involved in decision-making (ranging from local to federal levels). Environmental concerns focus on land-water interactions, managing flooding and water levels, maintaining food web stability and integrity, and promoting responsible boating (CNY-RPDB 2004). Management concerns for socio-economic components are generally poorly defined, but focus on threats to tourism and recreation as major contributors to the regional economy and responding to the concerns of individual landowners, organized stakeholder groups, and local communities. Managers devote

significant time and resources towards mitigating conflicts between stakeholder groups, which are primarily identified through passive listening.

Stakeholder Concerns

Stakeholder concerns are an important component of management systems. By identifying the diversity of stakeholder perspectives in socio-ecological systems, students gain a broader appreciation for how management decisions are influenced by and impact different aspects of society. Within socio-ecological systems, there is usually a continuum of stakeholder concern and involvement in watershed issues from very involved to disinterest. This is often directly related to the extent of a stakeholder's interactions with the socio-ecological system, including but not limited to type and amount of recreational lake use, location of residence within the watershed, and perceived strength of relationship between lake and livelihood. Interests among stakeholders are often highly diverse, with individuals sharing overlapping concerns on some issues but conflicting concerns on others.

Within the OLS, communication of stakeholder concerns to management and policy makers is primarily limited to a few key stakeholder groups. These stakeholder groups are often comprised of anglers, which are concerned about perceived differences between historical and current conditions and conflicts between anglers targeting different species. Additional stakeholder concerns are less understood.

EVALUATING POSSIBLE OBJECTIVES AND IDENTIFYING ACTIONS

After the context for the socio-ecological system has been described, the next step is to articulate probable fundamental and enabling objectives, and identify logical alternative primary actions to achieve these objectives. Throughout this process, one should anticipate collateral/subsequent impacts that can arise from management actions and identify mitigating actions to minimize creation of additional stakeholder concerns as a result of management. By default, social and ecological components will become increasingly focused as specific primary actions and collateral/subsequent impacts are identified to achieve individual enabling objectives. It is important to continue thinking broadly about cause-effect relationships that may not be initially apparent or well understood.

Fundamental Objectives

Fundamental objectives represent the main elements needed to actualize desired future conditions, and should reflect the need for management and what managers hope to accomplish through management actions. Fundamental objectives can be described qualitatively or quantitatively, but should aid decision making by focusing time and resources on enabling objectives and interventions that have a positive effect on achieving the desired future condition. Identifying fundamental objectives is often difficult because many students and managers are trained to find solutions to specific problems. Often these individuals have action bias, gravitating toward enabling objectives and actions, which for some are the extent of their concept of management's focus. Fundamental objectives, in contrast, should be used as a

benchmark that alternative enabling objectives and actions are evaluated against for their potential to achieve the desired future condition.

One fundamental objective to achieve the desired future condition for the OLS is ***to maintain/develop feedbacks between regional environmental quality and socio-economic well-being through creation and maintenance of opportunities that meet diverse stakeholder interests.*** Though this objective is generic, it helps managers focus on which enabling objectives and interventions contribute to this objective and aid in achieving the desired future condition. In future management cycles, this fundamental objective should be refocused and/or expanded to reflect quantifiable objective(s) achieved within a specific time frame. For instance, strong feedbacks between environmental quality and socio-economic well-being should be emphasized, while weak feedbacks should be given less priority.

Enabling Objectives

Enabling objectives identify the ecological and sociological conditions that enable achievement of the fundamental objective(s) and help focus specific management interventions and actions that should be taken. Managers and students are often most comfortable with this stage of the management cycle because enabling objectives are less abstract than fundamental objectives and desired future conditions and provide clear indicators to evaluate successful achievement of objectives. Additionally, enabling objectives tend to focus on a specific aspect of the socio-ecological system, and moves closer towards identifying actions and interventions, or in other words "what should be done." However, identifying how discrepancies

between the desired future condition and current conditions lead to management and stakeholder concerns and fundamental objectives is necessary to help create a broad vision for the socio-ecological system, which builds awareness of diverse interactions between social and ecological components incorporated into the Manager's Model. This can help prioritize enabling objectives and weigh competing objectives based on their importance in the context of broader objectives and goals.

One broad enabling objective for the Oneida Lake fishery is to ***maintain and improve the diversity and quality of fishing opportunities for resource users from diverse ages, ethnicities, and socioeconomic backgrounds.*** This enabling objective helps to identify and weigh different actions and interventions necessary to achieve the desired future condition, by acknowledging gaps between the desired future condition and current conditions within the lake. Specifically, it addresses that socio-ecological conditions within the lake are changing, and socio-ecological resilience to these changes requires a diverse stakeholder base that value the lake for multiple reasons. This is achieved through actions and interventions that build the resilience of the ecological and social components of the fishery by strengthening the fish community and improving the fishery's social and economic value. Ecological resilience pertains to many aspects of the ecosystem, including sustainable recruitment of young fish relative to harvest, stability of ecosystem structure and function, and water quality. Social resilience pertains to many aspects of the socioeconomic system, including awareness and interest in fishing for multiple species, easy access to the fishery (*e.g.* boat launches and fishing piers), and retention and recruitment of stakeholders. These enabling objectives aid in the identification of specific actions and interventions that

should be pursued to build feedbacks between the fishery and socioeconomic well-being (*i.e.* fundamental objective).

Primary Actions/Interventions

Primary actions/interventions represent specific actions that managers may or may not pursue to achieve enabling objectives, and should be identified and their feasibility evaluated through research and monitoring. Multiple alternatives should be considered, as well as the potential for actions to lead to collateral/subsequent impacts, which can create new stakeholder concerns. The action selected will depend on the state of the ecological or social component of interest and available resources required for execution, and can include active management, passive management, or no management. Student research often informs the management system through this component by evaluating the feasibility and impact of different actions/interventions to achieve enabling objectives.

Management decisions to execute actions impacting the Oneida Lake fishery are primarily made by the NYS-DEC, and active management is common. Regulations are commonly used to limit human activities and associated impacts on the environment and include but are not limited to harvest by anglers, point and non-point loading of nutrients and sediments into tributaries, and boating practices. Restoration and supplemental actions are used to enhance environmental conditions and include habitat restoration, stream bank stabilization, and fish stocking. Similarly, environmental conditions are enhanced by reducing or removing undesired species, such as Double-crested Cormorants (*Phalacocorax auritas*) and non-native species

(*e.g.,* water chestnut (*Trapa natans*)). Social actions focus on promoting the fishery to improve participation and increase stakeholder valuation of the resource, including active outreach to stakeholder groups, development of education programs to improve adult and youth literacy about interactions between the lake and watershed, and improving access through fishing piers and boat launches.

Collateral/Subsequent Impacts

Management actions/interventions often have collateral and subsequent effects beyond accomplishing enabling objectives, which can have both positive and negative impacts. Collateral impacts occur at the same time as primary actions/interventions, while subsequent impacts occur as a consequence of achieving objectives. Anticipating potential collateral/subsequent impacts is important when selecting between alternative primary actions/interventions and can help to develop mitigating actions that minimize these impacts. By identifying collateral/subsequent impacts of primary actions or interventions, students gain experience thinking about complex consequences to ecological and social components of the management system by anticipating direct and indirect effects of decision making.

Cormorant hazing on Oneida Lake provides a good example to illustrate how collateral/subsequent impacts can manifest in response to management actions. During the 1980s, cormorants began nesting on Oneida Lake and large flocks used the lake during their fall migrations (Jackson *et al.* 2012). Managers and stakeholders became concerned that cormorants could have negative effects on sport-fish populations, which was confirmed through research and monitoring. A two-fold

management action was developed to reduce consumption of sport-fish by cormorants, and included limiting: 1) the number of birds nesting by oiling eggs, and 2) the number of birds on the lake through hazing programs. Through this management plan, the enabling objective to maintain the quality of the fishery was achieved as cormorant use of the lake was reduced and consumption of sport-fish decreased. However, collateral/subsequent impacts emerged, resulting in a new set of stakeholder concerns. A limited number of stakeholders were sympathetic to cormorants and raised concerns about the humaneness of destroying eggs (*i.e.* collateral impact). Additionally, the hazing program did not cull birds, but pushed them onto nearby lakes, thereby creating a new set of stakeholders concerned about impacts of cormorants to nearby lakes (*i.e.* subsequent impact).

Mitigating Actions

Mitigating actions are proactive or reactive management actions designed to minimize collateral/subsequent impacts and reduce the creation of additional stakeholder concerns. As noted above, anticipation of collateral/subsequent impacts to primary actions/interventions is critical so that mitigating actions are already in place when collateral/subsequent impacts arise. Anticipation of collateral/subsequent impacts to primary actions/interventions and proper mitigating actions can prevent additional stakeholder concerns.

Examples of mitigating actions are common within the OLS. For example, in 2010 federal funding for cormorant hazing was not continued, raising serious stakeholder concerns about the potential for cormorants to negatively impact fish

populations. The NYS-DEC developed a management action to allow citizens to participate in cormorant hazing, but anticipated there was a high likelihood that this could result in collateral/subsequent impacts and raise additional stakeholder concerns (*e.g.* harassment of additional bird species and personal property damage). A mitigating action was developed, requiring that all individuals interested in participating in cormorant hazing undergo a training module and sign a waiver removing the NYS-DEC from liability of incidents associated with the hazing program. These mitigating actions have been successful and no additional stakeholder concerns have emerged as a result of citizen hazing programs.

WHERE DOES MY RESEARCH INFORM ONEIDA LAKE MANAGEMENT?

In the completed Manager's Model (Figure 4.1) for the OLS, research and monitoring provide the critical link of evaluation that allows adaptation across management cycles. By identifying historical and current conditions, research and monitoring can evaluate whether primary actions/interventions are accomplishing enabling objectives, thereby influencing the evolution of management and stakeholder concerns. Research and monitoring provide an unbiased method to test the validity of assumptions and reduce uncertainty, further improving the ability of managers to make informed decisions after weighing the feasibility of alternative management actions and effects on conflicting stakeholder interests.

My dissertation research focuses on understanding how multiple ecosystem changes within OLS influence fish populations and community dynamics. Ecosystem changes include greater predator and prey diversity, increased water clarity, and an

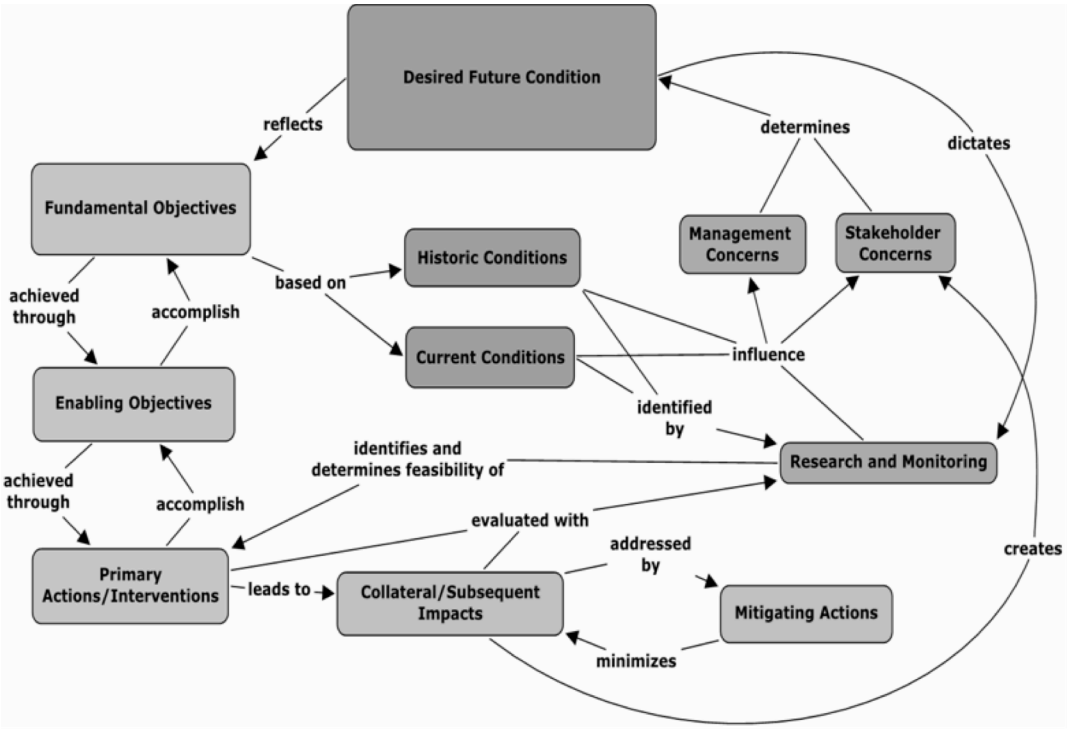

Figure 4.1. Manager's Model for the Oneida Lake socio-ecological system. Major ecological and social components indicated with boxes. Connections between boxes indicate the direction of information flow and the perceived relationship between components.

expansion of littoral habitats. The primary finding of this research is that understanding and predicting ecosystem dynamics within Oneida Lake have increased in complexity. Population and community dynamics are increasingly being driven by multiple habitats, especially littoral habitats. Interactions between predators and prey are no longer limited to walleye and yellow perch, but include smallmouth bass, largemouth bass (*Micropterus salmoides*), white perch (*Morone americana*), and gizzard shad (*Dorosoma cepedianum*). Ultimately, much of my research and others suggest that the ecological structure and function of Oneida Lake have changed. Though this research is inherently ecological, the results influence both social and ecological components of my Oneida Lake Manager's Model.

The most obvious place my research informs the management cycle is by evaluating the current research and monitoring programs on the lake and developing mechanisms to explain observed trends. This knowledge is then used to identify current ecological conditions within the lake and places them into context with historical conditions. This in turn influences both management and stakeholder concerns, and can reduce or increase the intensity of conflicts between stakeholder groups targeting different fish species. By building a better understanding of how the Oneida Lake ecosystem functions, my research also identifies and determines the feasibility of alternative primary actions/interventions and evaluates the potential for collateral/subsequent impacts. Current research suggests the feasibility to manipulate the lake ecologically to a desired state are likely limited, as the lake has undergone major ecosystem changes, and transitioned from a eutrophic state to a mesotrophic state (Mayer *et al.* in press). However, primary actions should be encouraged to raise

awareness among stakeholders about the changing lake conditions and recreational opportunities to develop mechanisms within the socio-ecological system to build value of the lake as an ecological, social, and economic asset to the region. I suspect a limited allocation of resources to develop an understanding of stakeholder values, perceptions, and satisfaction could produce high quality information (Hansen and Jones 2008) that would help focus efforts to increase the lake as an asset to the region. Additionally, this information would have a major impact on the management of the OLS by reducing uncertainty about stakeholder concerns and informing management concerns regarding stakeholders.

THE VALUE OF MANAGER'S MODELS TO EDUCATION

Manager's Models provide a useful framework for identifying and incorporating ecological and social components into fisheries management. As a teaching tool, this exercise does not attempt to replace traditional training in fisheries sciences, but instead builds on these foundations by raising awareness of how feedbacks occur within socio-ecological systems. This prevents the curriculum from training "jacks of all trades, masters of none" (Hubert 2011), but instead embraces specialization by identifying where within the broader socio-ecological system a student's particular expertise can make the greatest contribution. Therefore, fisheries students from diverse backgrounds and interests can find value and learn from this and similar exercises that develop the skills necessary to address complexity in a rapidly changing world.

This paper presents one perspective of how constructing a Manager's Model can be used as a learning exercise to raise student awareness about how/where science informs management in socio-ecological systems. In constructing the Manager's Model, I conceptualized "my" model of how the OLS works, which helped me to position my work within that system. Everyone has his or her own nuanced perspective of how the management system works, even if not formally articulated. Processes that facilitate integrating multiple perspectives into a shared model of the management system could improve application of Manager's Models as a teaching tool. This could be done through graduate seminars, undergraduate group projects, or through a participatory process involving scientists, managers, and stakeholders. These experiences develop the interpersonal and professional skills necessary to address the challenges of decision making in complex socio-ecological systems. Hopefully, through student presentations of the Manager's Models to managers and stakeholders for purposes of gaining feedback and seeking improvement, this learning process can continue from the students to the practicing fisheries scientists and managers to make real changes where it is needed most.

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